INVASIVE PERENNIAL SPECIES IN AN AGRICULTURAL AREA OF THE WESTERN CAPE PROVINCE: DISTRIBUTION AND RELATIONSHIP WITH VARIOUS LAND-USE TYPES

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Declaration

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature……………………   Date…..…………………

SUMMARY

This project consists of two botanical investigations in an agricultural area of the Western Cape Province. A farm known as De Rust, in the Elgin Valley, was used to sample the geographic location, density, height and life stage of six prominent invasive plant species in various land-use categories.

In the first investigation, the density, height and age structures of the six invasive species populations were analyzed. The density distribution of the six species was also displayed cartographically. Species were then ranked according to the potential threat that they pose to the conservation of the remaining natural areas on the farm. Results indicated that *Acacia mearnsii* and *Acacia saligna* are the major invaders at De Rust and that *Hakea sericea* can be considered as an emerging invader.

The second investigation explores the statistical relationship between the various land-use categories and density, height and age of the six prominent invaders identified in the first investigation. The log-likelihood ratio analysis of observed frequencies resulted in statistically significant ($P<0.01$; P-values range between 1.35×10^{-3} and 2.7×10^{-224}) relationships between certain land-use types and certain invasive species. A conclusion was reached that it could be useful to include land-use categories in simulation models of invasive plant species distribution and spread.

OPSOMMING

Hierdie projek behels twee botaniese ondersoeke in ‘n landbou gebied van die Weskaap. Die plaas bekend as De Rust, in die Elgin Vallei, was gebruik vir die versameling van data te doen met die geografiese ligging, plant digtheid, lengte en lewens stadium van ses prominente indringer plant spesies in verskeie landgebruik kategorieë.

Die digtheid, lengte en ouderdomstruktuur van ses indringerspesies was in die eerste ondersoek geanaliseer. Die verspreiding van digtheid was ook in kaarte uitgelê. Spesies was daarna volgens hulle potentiële dreiging teen die bewaring van oorblywende natuurlike dele van die plaas in ‘n rangorde geplaas. Resiltate dui aan dat *Acacia mearnsii* en *Acacia saligna* die belangrikste indringer plante op De Rust is en dat *Hakea sericea* as ‘n opkomende indringer beskou kan word.

Die tweede ondersoek kyk na die verhouding tussen verskeie grondgebruik kategorië en die digtheid, lengte en ouderdom van die ses prominente indringer spesies wat in die eerste ondersoek identifiseër is. ‘n Log tipe ratios ontleding van bewaarde frekwensies het ‘n statisties belangrike uitkoms gehad ($P<0.01$; P-waardes tussen 1.35×10^{-3} en 2.7×10^{-224}) vir die verhoudings tussen sekere grondgebruik tipes en sekere indringer spesies. Die gevolgtrekking was dat dit handig mag wees om grondgebruik kategorieë in simulasies van indringer plant verspreiding te gebruik.

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CHAPTER 1: GENERAL INTRODUCTION

The first published calculations of invasive alien plant effects on streamflow in South African catchments date back to the 1970s (Kruger 1977). They indicated that invasions by these plants were already having a serious influence in many areas. These predictions that invasive alien plants would use significant amounts of water were a major reason for the establishment of South Africa's Working for Water programme, which aims to safeguard water resources by clearing these plants (Gorgens and van Wilgen 2004). Richardson and van Wilgen (2004) propose that most South African research on the topic of invasive plants has explicitly addressed the connection between alien plant invasions and ecosystem goods and services affiliated with water resources. Some of this research has been groundbreaking, for example the detailed appraisal of costs and benefits of the commercially significant but invasive tree *Acacia mearnsii* in South Africa (de Wit *et al.* 2001), is unique at a global scale (Richardson *et al.* 2004). However, a review of the mechanisms of invasions (Levine *et al.* 2003) highlights the deficiency of studies aimed at identifying factors and processes involved in invasions and effects on ecosystems. While Macdonald (2004) agrees that our understanding of the impacts of invasive alien plants in South Africa is fragmentary at best, and is mainly confined to the fynbos biome, he states that scientists now have a good understanding of the process of alien plant invasion. Macdonald (2004) continues by proposing that we have a fairly clear idea of the extent and species involved in the problem in South Africa, but our comprehension of links between ecosystem structure, processes and functioning and the capacity of these ecosystems to provide goods and services is still very basic. According to Richardson and van Wilgen (2004), invasive alien plants are concentrated in the Western Cape, along the eastern seaboard, and into the eastern interior, but they argue that there is a deficiency of accurate data on abundance within these regions.

It is clear that the study of invasive alien pants can be tackled from many different angles, and many authors (Milton 1980; Richardson *et al.* 1989; Musil and Midgley 1990; Vitousek 1990; Musil 1993; Holmes and Cowling 1997; Wilcove *et al.* 1998; Parker *et al.* 1999; Le Maitre *et al.* 2000; Van den Berkt 2000; Byers *et al.* 2001; Crooks 2002) have endeavoured to unravel the consequences of invasive alien species presence in natural and semi-natural ecosystems. However, Richardson and van Wilgen (2004) state that most South African research on alien-plant impacts has focused at small spatial scales (plots or communities), and most of this work pertains to the fynbos biome. The topic is a multi-scale puzzle, encapsulated in the equation I = R x A x E (Parker *et al.* 1999). Impact (I) is intuitively the product of the (potentail) geographic range of the invader (R), its (potential) abundance or density (A), and the effect (E) of an invader or the ascertainable impacts at the smallest spatial scale.

Richardson and van Wilgen (2004) state that besides their effects on agriculture, forestry and human health, biological invasions are also widely recognized as the second-largest global threat (after direct habitat destruction) to biodiversity (Wilcove *et al.* 1998; Walker and Steffen 1999). Vila and Pujadas (2001) provide support for this statement and quote evidence of analyses at the regional level which have demonstrated that disturbed and man-made areas are invaded more than pristine areas (Hobbs and Huenneke 1992; Pysek 1994). They provide examples such as roadsides and agroecosystems, which, they say, harbour a great number of alien species. Vila and Pujadas (2001) also state that changes in land-use are important means by which aliens spread and increase, providing the example that agricultural intensification in the USA has lead to an increased abundance of aliens in adjacent habitats (Boutin and Jobin 1998). Fragmentation is proposed as another factor enhancing plant invasions (Saunders *et al.* 1992; Brothers and Spingarn 1992). Likewise, transport networks (e.g. highways, railways, etc.) also enhance immigration rates of new species and the spread of already existing ones (Ernst 1998). Areas adjacent to roads and railways have been found to be rich in alien species at the regional scale, even within nature reserves (Tyser and Worley 1992; Pysek 1994). Rouget and Richardson (2003) state that, surprisingly, land-use was not identified as the major barrier to invasion of the pines in their study and that there were some indications that spread (of pines) was reduced in transformed habitats (notably cultivated fields).

Intrigueing results from a comparison of the effects of invasive alien species with other forms of transformation (Latimer *et al.* 2004), including agriculture, forestry and urbanization, suggests that agriculture is by far the most important agent for transformation, in area and in severity of species loss. Latimer *et al.* (2004) also propose that forestry and urbanization cause relatively high species loss where they occur and that invasive alien plants are widespread, but have the *least* severe effects on biodiversity where present. Their reasoning for such an unusual statement is based on the findings of their study in the Kogelberg Nature Reserve, where the total proportions of the study area that have been transformed are 34.4% for agriculture, 4.1% for forestry, 3.6% for high and medium density aliens and 2.6% for urbanization. They argue that agriculture affects common species disproportionately, whereas forestry and invasive alien plants influence species in direct proportion to their prevalence. Therefore, invasive alien plants have had by many measures a smaller effect on diversity than other forms of transformation. However, they conclude that invasive plants may pose the greatest continuing threat to diversity and rare species if they are allowed to persist and spread to their full potential.

Six perennial invasive species were selected to form the basis of our study. They were the invasive species judged most abundant at De Rust and the second chapter of the project deals with the cartographic display of their distribution and abundance. The following descriptions (Henderson 2001) highlight important features of the history and morphology of the six study species.

Acacia saligna (Labill.) H.L. Wendl. (= *A. cyanophylla* Lindl.)
In 1848, the first Port Jackson seeds were planted to stabilize the sand on the new road from Cape Town to Bellville. Today it can be found inland and along the coast from the Orange River to Kosi Bay.

Table 1.1. Description of *Acacia saligna*.

Common name	Port Jackson
Description	Unarmed, evergreen shrub or tree 3-7(-10) m high with a willow-like appearance; stems usually deformed by large, brown irregularly shaped swellings or galls (caused by an introduced rust fungus).
Leaves	Phylloides, blue-green turning bright green, up to 200 mm long and 10-50 mm wide, slightly erect to pendulous, with a single midvein, wider and wavy on young plants.
Flowers	Bright yellow, globular flowerheads, August-November.
Fruits	Brown pods with hardened, whitish margins.
Invades	Fynbos, woodland, coastal dunes, roadsides, watercourses.
Origin	SW Australia
Invasive status	Transformer; declared invader (category 2).

Acacia mearnsii (De Wild.)

The black wattle was originally brought to South Africa in the 19th century by an immigrant farmer named John Vanderplank. He imported seeds from Tasmania to his farm near Camperdown in Kwa-Zulu-Natal.

Table 1.2. Description of *Acacia mearnsii*.

Common name	Black wattle
Description	Unarmed evergreen tree 5-10(-15) m high; branchlets shallowly ridged; all parts finely hairy; growth tips golden hairy.
Leaves	Dark olive-green, finely hairy, bipinnate; leaflets short (1.5 – 4.0 mm) and crowded; raised glands occur at and between the lunctions of pinnae pairs.
Flowers	Pale yellow or cream, globular flowerheads in large, fragrant sprays, August-September.
Fruits	Dark brown pods.
Invades	Grassland, forest gaps, roadsides and watercourses throughout its range.
Origin	SE Australia and Tasmania
Invasive status	Transformer; declared invader (category 2).

Acacia longifolia (Andr.) Willd.

First introduced to South Africa in 1827, Rooikrans was only reported as a problem plant in 1945 when it had invaded Houwhoek and Mitchells passes.

Table 1.3. Description of *Acacia longifolia*.

Common names	Rooikrans, Long-leaved wattle
Description	Unarmed evergreen shrub or spreading tree 2-6(-10) m; stems usually have spherical outgrowths or galls (caused by an introduced wasp); the galls are green turning brown, replacing flower and leaf buds. Galls are smooth as opposed to knobbly in *Acacia pycantha.*
Leaves	Phylloides, bright green, up to 180 mm long, 2-5 prominent longitudinal veins.
Flowers	Bright yellow, cylindrical flowerheads up to 50 mm long and 7 mm wide, in the axils of the leaves, July-September.
Fruits	Pale brown pods, beaked apically, constricted between seeds.
Invades	Fynbos, woodland, watercourses.
Origin	SE Australia and Tasmania
Invasive status	Transformer; Declared weed.

Hakea sericea Schrad. & J.C. Wendl.

Imported in 1830, *H. sericea* was used fror hedges and to stabilize loose sand. At one stage invasion in the Western Cape had covered 14% of mountain fynbos.

Table 1.4. Description of *Hakea sericea*.

Common name	Silky hakea
Description	Much branched, very prickly shrub or tree up to 5m high; young twigs covered in short, fine hairs, older stems glaborous.
Leaves	Dark green to grey-green, glaborous, needle-shaped, up to 40 mm long, sharp pointed.
Flowers	Cream, small, in leaf axils, June-September.
Fruits	Wooden capsules, 25-30 mm long, 20-25 mm wide with two apical horns, purplish-brown with paler markings, turning grey, surface thick and wrinkled; splitting into two equal valves, each containing one winged seed.
Invades	Mountain fynbos.
Origin	SE Australia
Invasive status	Transformer; Declared weed.

Eucalyptus grandis W. Hill ex Maiden

Table 1.5. Description of *Eucalyptus grandis*.

Common name	Saligna gum
Description	Tall evergreen tree with shaft-like trunk, 25-55(-72) m high; bark smooth, except butt up to 4m, peeling in long thin strips to expose a powdery, white, grey-white or blue-grey surface.
Leaves	Dark green and glossy above, paler below; adult leaves130-200 mm long, similar to juvenile leaves.
Flowers	Cream with long-exserted stamens, buds up to 8 mm long, pear shaped with conical lids, peduncles flattened, April-August.
Fruits	Capsules, brown with bluish-grey bloom, pear shaped, 7-10 mm long, with protruding valves that arch inwards.
Invades	Forest gaps, plantations, watercourses, roadsides.
Origin	E and NE Australia
Invasive status	Transformer; Declared invader (category 2).

Pinus pinaster Aiton

The cluster pine was one of the first pines used in commercial plantations in South Africa when it was introduced in 1825 by the French Hugenot settlers. The worst cases of invasions occur around Franschoek in the Western Cape where the Hugenots established the first plantations.

Table 1.6. Description of *Pinus pinaster*.

Common name	Cluster pine
Description	Coniferous tree 8-15(-30) m high; conical when young, becoming cylindrical with a tall bare trunk when older; bark reddish brown, deeply cracked into plates.
Leaves	Needles, dull grey-green, in bundles of two, long (80-240 mm), thick and rigid.
Cones	Initially purple, turning light brown, woody, conic-ovoid, 90-180 mm long, shortly stalked, often clustered and persistent; cone scales have a distinct ridge with a short, hard, curved point.
Invades	Mountain and lowland fynbos.
Origin	Mediterranean
Invasive status	Transformer; Declared invader (category 2).

An alternative method of invasive plant research is the computerised simulation model (Richardson *et al.* 2000; Shafii *et al.* 2003; Rouget *et al.* 2004). Such models rely on mathematical relationships between invasive plants and the environment to predict outcomes of alien plant presence in landscapes. Predictions can be made at various scales, depending on the nature of the data that derived the mathematical relationships forming the basis of the simulation. Richardson and van Wilgen (2004) propose that data on the geographical distribution of invasive alien plant species provide information at one level and that it is critical to know how abundant or dense invasive species can become at finer scales. However, Gorgens and van Wilgen (2004) warn that researchers face the problem of scaling up from site-specific observations. Rouget and Richardson (2003) provide examples of previous studies that attempted to simulate the spread of invasive species. They provides criticism for Schupp and Fuentes (1995) who focused on local seed dispersal using spatial patterns of juveniles and did not always consider the effects of environment. Spatial patterns of invasion result from many diverse interacting factors, including biological attributes of the invader, species response to the abiotic environment, biotic interactions and human activities (Richardson 2004). Rouget *et al.* (2004) found that the pattern of invasion, as well as the relative significance of physical and environmental factors, has changed considerably over time. They resolve that invasion pattern, specifically of pines, is more a function of propagule dispersal (short- and long-distance) than habitat suitability and quote Richardson *et al.* (2000) who suggested the possibility that alien species might perform better than native ones in fragmented habitats due to their higher seed production and dispersability. In addition, they suggest that intense disturbance, notably fire, is probably the only requirement for conversion of isolated pine individuals to dense stands. These stands later function as seed sources for additional expansion within other landscape units Rouget *et al.* (2004).

Richardson and van Wilgen (2004) propose that there is a scarcity of well-documented accounts of the impacts of invasions, and of robust models enabling us to scale-up our predictions of results on the delivery of ecosystem goods and services. The development of that kind of model demands a better understanding of the results of invasions at fine scales. They advise caution because outcomes can vary with species, soil type and disturbance regime, and thus further complicate the task. A better understanding of the process would require including changes in land-use and habitat fragmentation in our models Rouget *et al.* (2004). For this reason, our study aims to provide evidence that a relationship exists between land-use types and invasive perennial plant species density, at a relatively fine scale, in an agricultural environment. This ultimate goal of the project is presented in Chapter 3.

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CHAPTER 2

An evaluation of the threat posed by invasive perennial weed species in an agricultural area of the Western Cape Province.

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Introduction

Estimates of woody alien species abundance suggest that between 1.7 million ha (van Wilgen *et al.* 1998) and 10 million ha (Versverld 1998) of South Africa and Lesotho have been aggressively invaded by only a few exotic species. Ninety percent of the invasion problem can be attributed to about 15 species (including Australian *Acacia*, *Eucalyptus* and *Hakea* species, and European and American *Pinus* and *Prosopis* species) (van Wilgen *et al.* 1998). Dense stands of these alien trees threaten the biodiversity and functioning of natural ecosystems, as well as significantly lowering water yields (van Wilgen *et al.* 1996; Le Maitre *et al.* 2000). These species are estimated to use 3300 million m^3 of water each year in South Africa, which is almost 7% of the runoff of the country (van Wilgen *et al.* 1998). Quantifying the overall effect of invasive species presence in a landscape is complex, because effects can be on individuals, population dynamics, communities or ecosystems (Parker *et al.* 1999). Nonetheless, an estimate of the impacts of invasive plants suggests that they result in billions of rands of lost revenue (van Wilgen *et al.* 1997).

One of the more important impacts, from an ecological perspective, is the reduction of biodiversity (MacDonald *et al.* 1986). Exotic plantations in South Africa are generally perceived to support lower biodiversity than indigenous forests and this has been confirmed in studies of invertebrates (Donnely and Giliomee 1985; Manders 1989; Samways *et al.* 1996; Ratsirarson *et al.* 2002), plants (Cowling *et al.* 1976; Richardson *et al.* 1992) and birds (Winterbottom 1968, 1972; Armstrong and van Hesbergen 1995, 1996). Plant architecture can sometimes be more important in influencing epigaeic invertebrate assemblages rather than whether the plant is exotic or indigenous (Samways and Moore 1991). Invasion by woody plants can change the canopy structure (Versveld and van Wilgen 1986), leaf litter quality and composition (Milton, 1980) and can produce dense and impenetrable thickets that impede the flight of insects (MacDonald *et al.* 1986; Steenkamp 1996). Increasing density of upper storey vegetation shades out the understorey vegetation and can influence moisture content of the soil (Samways *et al.* 1996). For example, soil under *Acacia mearnsii* becomes desiccated more quickly than when under grass (Versveld and van Wilgen 1986). Other woody invasives inhibit understorey vegetation by allelopathic activity, when harmful chemical compounds are released from their decomposing leaf litter (Al-Naib and Al-Moussawi 1976; Lisanework and Michelson 1993). For example, leachates from the first days of *Eucalyptus* litter decomposition were added to sand in which test plant seedlings were grown and a strong allelopathic activity was observed (O'Connel and Sankaran 1997). To minimise these negative effects, the South African National Department of Agriculture introduced the Conservation of Agricultural Resources Act (CARA), Act No. 43 of 1983. Amendments promulgated in March, 2001 were necessitated by the accelerating deterioration of the country's natural resources due to invasion by exotic weeds (Klein 2002). The act states that declared weeds will no longer be tolerated on land or on water surfaces, neither in rural nor in urban areas.

In 1995, the Working for Water Programme was initiated countrywide by the Departments of Water Affairs and Forestry, Environmental Affairs and Tourism and Agriculture in South Africa with the objective of clearing invasive woody plants and simultaneously creating employment opportunities (van Wilgen *et al.* 1998). Although there are considerable costs involved in controlling invasive plants, the potential benefits in terms of job creation, increased water yields and other ecosystem services outweigh these costs (van Wilgen *et al.* 1997). The long term success of alien clearing will depend on restoring functional ecosystems, as without this, cleared areas are prone to reinvasion and excessive soil loss due to erosion (van der Heyden 1998). The recovery of indigenous vegetation is therefore the best way to assess the success an alien plant removal programme (Holmes and van der Heyden 2000).

The Conservation of Agricultural Resources Act (CARA) states that alien clearing would lead to prevention of the weakening or destruction of water resources and protection of the vegetation. Therefore, controlling invasions of alien plant species can conserve production potential in an agricultural landscape. However, the first step in achieving this goal efficiently in any given farming area is to produce accurate maps of the distribution of the most common invasive perennial species. This will facilitate quantification of the extent to which species have invaded in terms of total area and the percentage of the total farm area. It would also enable the determination of the patchiness of each species' distribution. Examination of the age structure of invasive plant populations could provide useful information on their potential for further invasion. Finally, evaluation of the relative importance of each species, in terms of distribution and population age structure, enables them to be ranked according to the threat that they pose for further invasion. This information may then be used to identify priority species and areas for alien removal, ensuring that the process is as efficient and cost-effective as possible. The aim of this study was therefore to conduct such a mapping and prioritization procedure in an agricultural area in the Elgin valley in the Western Cape Province. The study farm is planted under vineyards and orchards, but also includes areas of pristine fynbos and semi-pristine renosterveld-fynbos transition vegetation.

Methods

Site description:

De Rust is a farm situated in the Elgin valley, near Grabouw in the Western Cape Province, South Africa. The 2600ha property is situated on the foothills of the Groenlandberg mountain range (19.10° E; -34.16° S) and contains an altitudinal gradient stretching from the lower mountain slopes (around 600m above sea level) towards the drainage basin in the valley bottom (around 250m above sea level). The natural vegetation in the area is described by the C.A.P.E. project as Elgin Fynbos/Renosterveld Mosaic, which is essentially Renosterveld with many Fynbos elements (Helme 2003). The agricultural activities undertaken on the property include vineyard and orchard cultivation, as well as small-scale livestock and game rearing. The majority of the property (1600 ha) was included in this study, and only the area on the southern side of the N2 highway, as well as some of the uninvaded steeper slopes of the Groenlandberg property border and were excluded.

Extent of species distributions:

The six most common invasive perennials within the De Rust property boundaries were selected in order to construct accurate maps of their distribution. These species were identified as the most abundant and widespread in a pilot survey of the farm. A handheld GPS reciever was then used to identify the location of stands of *Acacia saligna* (Labill.) H.L.Wendl., *A. mearnsii* (De Wild.), *A. longifolia* (Andr.) Willd. *Mimosaceae, Hakea sericea* Schrad. & J.C.Wendl. *Proteaceae, Eucalyptus grandis* W. Hill ex Maiden *Myrtaceae* and *Pinus pinaster* Aiton *Pinaceae* plants. At the location of each datapoint, the presence/absence, as well as the density, height and age structure of each of the 6 chosen species was estimated.

Cartography

The distribution of any objects can be displayed in maps constructed by GIS (Geographical Information Systems) computer software as long as the geographical co-ordinates of the objects are known. Distribution and population structure data were therefore entered into a spreadsheet (MS Excel) and then transferred to a GIS software package (ArcView 3.2) with which maps of distribution and density of each species were produced at a scale of 1:40 000.

Patchiness of distribution:

Rouget *et al.* (2004) found that, for dense patches of pines, it was impractical to map the locality of each plant as densities exceeded 200 pines per ha in many areas. Consequently, they mapped the boundaries of such patches using a GPS. We decided to follow a similar method of data collection, therefore transects were walked around the perimeters of stands of invasive species, as well as the perimeters of land-use units, and sampling of datapoints occurred along these perimeters. The distance between datapoints was not always constant and reflects the locations where stand density changed in comparison to adjacent datapoints. The maximum distance between datapoints did not exceed 100m. Each datapoint represents a certain area of invasion, however a point on a map contains no area. Therefore, Arcview 3.2 was used to calculate the total area invaded by each species. To achieve this, two approaches were employed. Firstly, a buffer was created around each datapoint with a radius value depending on the density of the stand, therefore size of the radius was assigned as an approximation of the area around the datapoint that was invaded. A 15 m radius, or buffer, was created around 'Sparse' stands (Density classes defined below). As stand density increased, buffer radius increased by 5 m for each consecutive category resulting in 20 m buffers for stands with 'Intermediate' density, 25 m buffers for 'Dense' stands and 30 m buffers for 'Very dense' stands. The result of the application of buffer areas resembles a string of beads, with the string representing the transect while the beads represent the invaded areas (Figure 1.1). Buffer areas could then summed as an estimate of the area invaded by a species. The ratios of buffer perimeters to buffer areas were calculated as a representation of patchiness. A greater perimeter to area ratio value for a particular species indicates a more patchy distribution.

Secondly, and most similar to the methodology of Rouget *et al.* (2004), polygons were created around the edges of buffered datapoints. This was nescessary, because in the case of very large stands of invasive trees, buffer areas may not accurately reflect the total area of the invasion. Polygons are adaptable shapes that can be used to trace the perimeter of transects and calculate the complete area contained within them (Figure 1.1). The resulting polygon areas were totaled for an alternative representation of the total area invaded by each species. The same method of calculating patchiness for buffers was used for polygons. Thus, ratios of polygon perimeters to polygon areas were calculated. A greater perimeter to area ratio value for a particular species would suggest a patchier distribution.

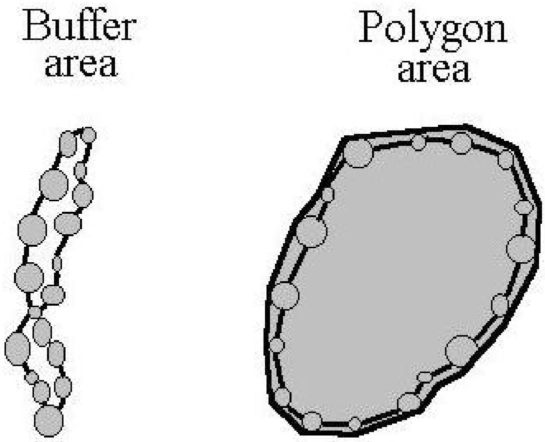

Figure 2.1. Conceptual representation of buffer and polygon areas. “Buffer area” shows dark lines (‘strings’) representing transect route between circles (‘beads’) representing buffer areas (grey filled). “Polygon area” shows outer dark line, representing polygon perimeter, encircling transect and datapoints with buffer areas (‘string of beads’). Total polygon area is represented by the grey filled area under “Polygon area”.

The buffer and polygon areas used to calculate the total area of invasion for each species are displayed in separate maps for each species (Appendix A, Figures 1-6).

Stand density was separated into four categories. ‘Sparse’ refers to areas where less than 5 individuals of a species were present. ‘Intermediate’ describes stands of between 5 and 20 individuals of a species. ‘Dense’ areas contained more than 20 individuals of a species and to classify an area as ‘Very dense’ meant that the stand was so dense that a person could not walk, or even see more than a few metres, into the area.

Population Structure

The life stage structure of each species was recorded in four categories. ‘Seedling’ refers to small plants (less than 20cm tall) that have recently germinated. ‘Sapling’ means young plants that had not reached reproductive maturity. ‘Adult(s)’ were established plants that did not show any signs of flowering or seed production and ‘flowering adults’ defined established plants that were in the process of producing flowers or seeds or on which there was evidence of old flowerheads. Stage categories were broadly structured so that they could also provide a rough approximation of plant age. The difference between life stage and the age of plants is that stage is a qualitative measure of a plants position in its life history cycle, while age is the quantitative measure of how long a plant has lived. Stage category frequency is therefore a rough representation of the population age structures of the selected invasive species at De Rust.

The heights of plants were recorded in seven categories. Areas classified as ‘<1m’ meant that all plants were shorter than 1m in height. Similarly, ‘<2m’ refers to areas where all plants were shorter than 2m in height. This type of classification was applied to areas where all plants were shorter than 3m (‘<3m’), 4m (‘<4m’) and 5m (‘<5m’) in height. When all plants were taller than 5m, the area was assigned to the ‘>5m’ category. The final category was ‘1 - >5m’ and defined areas where plants were found in a range of heights from 1m to greater than 5m tall. Rouget *et al.* (2004) used height as a surrogate of age. Therefore, height category frequency in our study could be interpreted as a measure of stand maturity, or the length of time that a stand has been present in the landscape.

Results

Extent of species distributions:

Arcview analysis showed that all species are distributed between 19.08° E & 19.13° E and-34.14° S & -34.19° S. These co-ordinates represent the sampling boundaries to the East, West and South. The northern sampling boundary is situated on the upper slopes of the Groenlandberg Mountains where no invasive species were found. The fine scale distribution and density of *A. saligna* (Appendix B: Figure 1), *A. mearnsii* (Appendix B: Figure 2), *A. longifolia* (Appendix B: Figure 3), *H. sericea* (Appendix B: Figure 4), *E. grandis* (Appendix B: Figure 5) and *P. pinaster* (Appendix B: Figure 6) stands were clearly different for each species. *A. saligna* (Appendix B: Figure 1), *A. mearnsii* (Appendix B: Figure 2), *A. longifolia* (Appendix B: Figure 3) and *P. pinaster* (Appendix B: Figure 6) are distributed throughout the farm area. *Eucalyptus grandis* (Appendix B: Figure 5) is found predominantly along farm boundaries and the railway line, while *H. sericea* (Appendix B: Figure 4) occurs almost exclusively in the northwestern corner of the property.

Patchiness of distribution:

The total farm area was calculated as 16.76 km² (approximately 1600 ha). The species that was encountered most frequently was *P. pinaster* (1032 records) and the most infrequently encountered species (160 records) was *H. sericea* (Table 2.1). Polygon areas of each species (Table 2.2), expressed as percentages of the total farm area (Table 2.3), show that *P. pinaster* takes up the most space on the farm (28.6%) and that *E. grandis* takes up the least space (5.6%). Buffer areas of each species (Table 2.2), expressed as percentages of the total farm area (Table 2.3), suggest that *A. saligna* takes up the most space on the farm. Polygon perimeter to area ratios show that *E. grandis* has the patchiest distribution, while buffer perimeter to area ratios were greatest and nearly equal for *A. longifolia*, *H. sericea* and *P. pinaster* (Table 2.3).

Table 2.1. Number of positive records of invasive woody species and their density at De Rust

Species	Records	Species density (records/km²)
Acacia saligna	737	44.0
Acacia mearnsii	963	57.5
Acacia longifolia	698	41.7
Hakea sericea	160	9.5
Eucalyptus grandis	296	17.7
Pinus pinaster	1023	61.0

Table 2.2. Total area and perimeter of buffers around data points and polygons containing stands of each invasive woody species at De Rust

	Acacia saligna	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
Buffer area (km^2)	2.1	1.2	0.8	0.2	0.7	1.2
Polygon area (km^2)	2.6	3.6	2.1	1.1	0.9	4.8
Buffer perimeter (km)	91.8	112	77.8	19.2	35.4	116.6
Polygon perimeter (km)	72.6	89	66.3	15.1	29.6	98.5

Table 2.3. Buffer and polygon areas expressed as percentages of the total farm area, as well as buffer and polygon perimeter (P) to area (A) ratios for invasive woody species at De Rust

	Acacia saligna	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
Buffers (%)	12.7	7.2	4.7	1.2	4.2	7.3
Polygon (%)	15.8	21.4	12.5	6.7	5.6	28.6
Buffers P:A	43.7	93.3	97.3	96.0	50.6	97.2
Polygon P:A	27.9	24.7	31.6	13.7	32.9	20.5

Population Structure:

Acacia saligna, *A. mearnsii* and *P. pinaster* populations were dominated by saplings i.e. more than 50% of individuals had not reached reproductive maturity (Figure 1.2). *Acacia longifolia* and *H. sericea* populations were dominated by adult plants i.e. more than 50% of individuals are capable of adding to the seedbank. The *E. grandis* population had a fairly even distribution across the stage categories (Figure 1.2).

Acacia saligna, *A. mearnsii* and *E. grandis* were more common in the taller height classes, but stands containing both tall and short plants were most common (Figure 1.3). *Acacia longifolia* stands were dominated by plants shorter than 5m and *H. sericea* stands were mostly shorter than 3m. *Pinus pinaster* stands were split between containing, either tall plants and short plants together, or only short plants i.e. less than 3m tall (Figure 1.3).

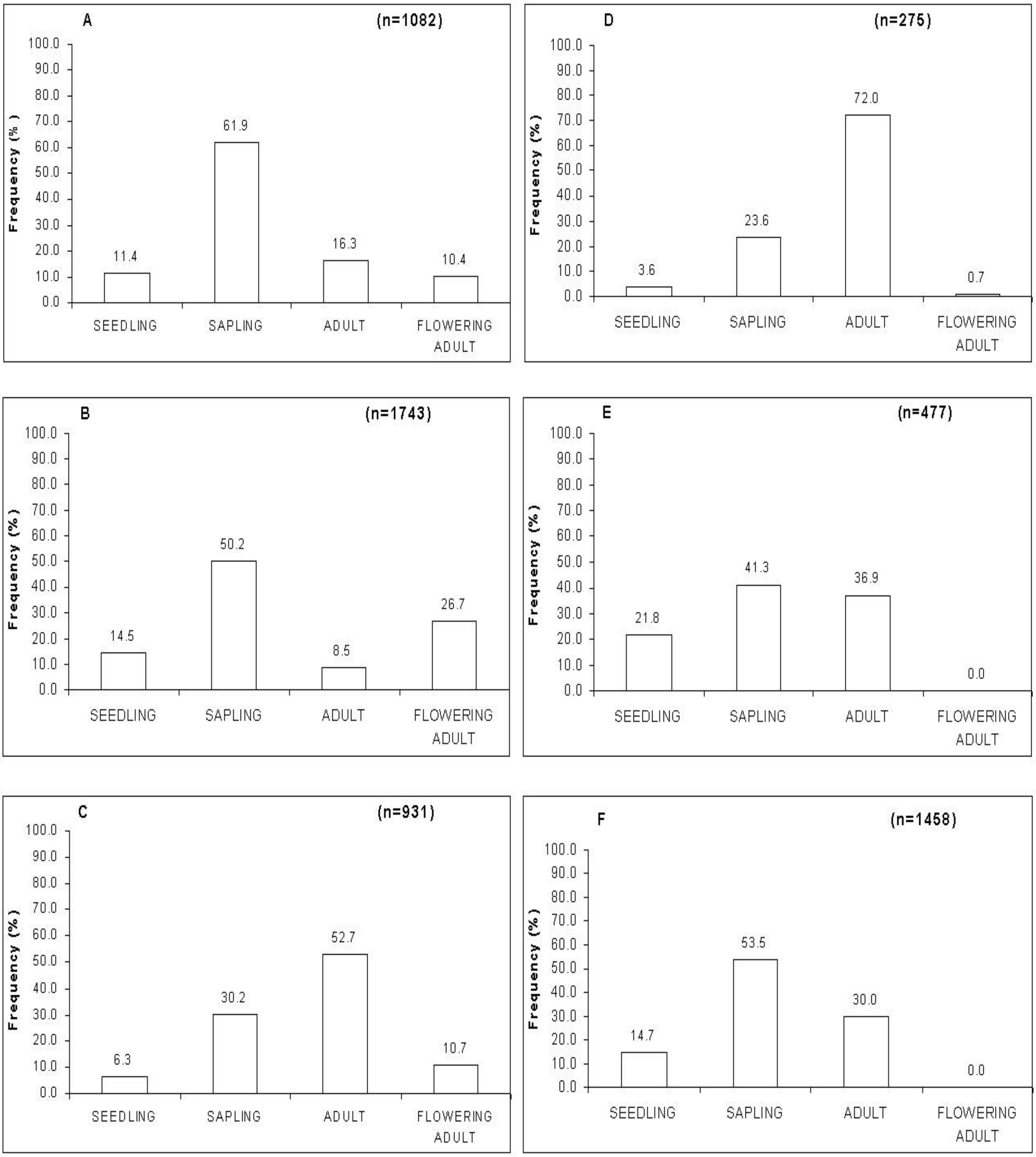

Figure 2.2. Frequency of stage categories for each species; A, *A. saligna*; B, *A. mearnsii*; C, *A. longifolia*; D, *H. sericea*; E, *E. grandis* and F, *P. pinaster*.

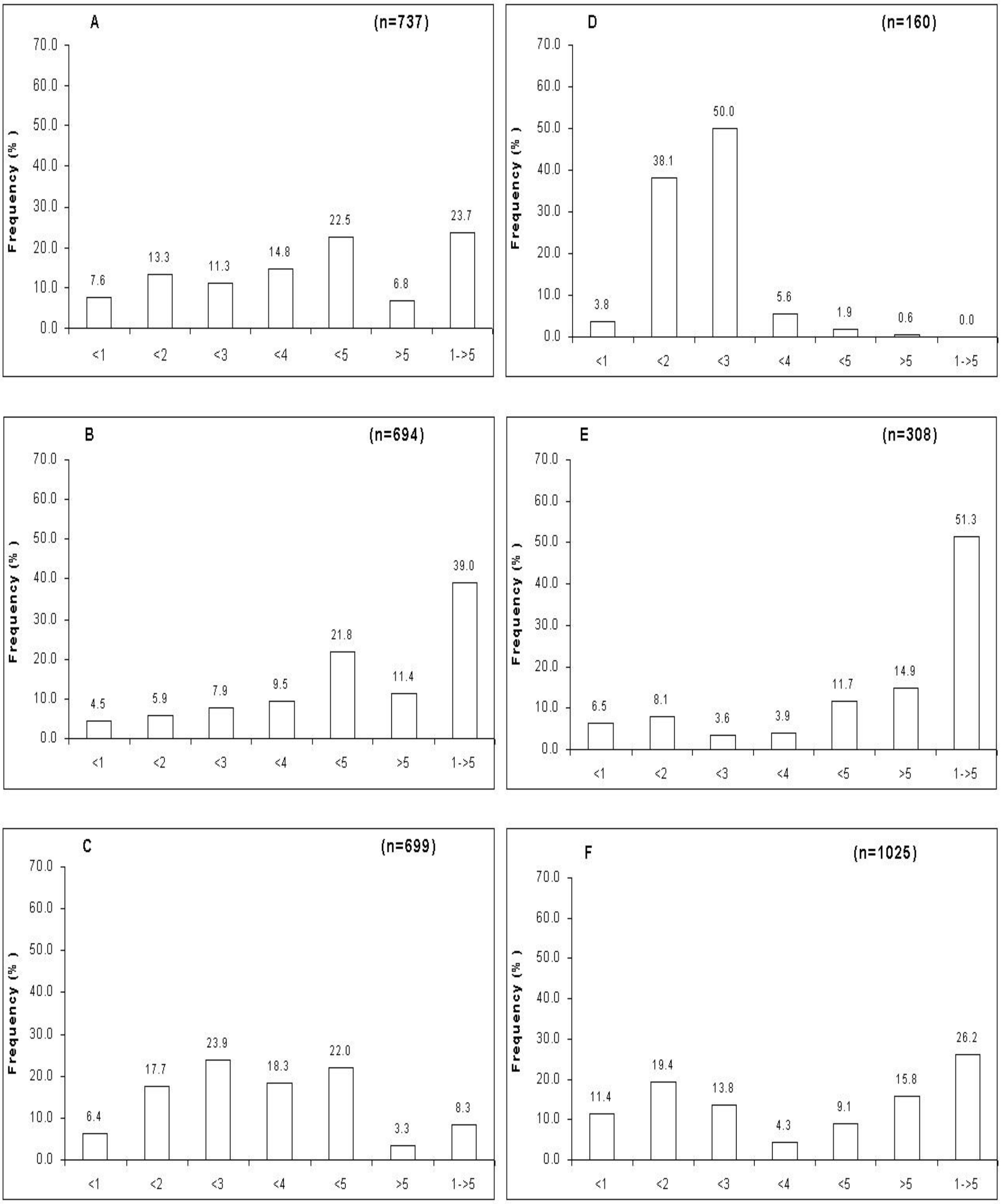

Figure 2.3. Frequency of height categories for each species; A, *A. saligna*; B, *A. mearnsii*; C, *A. longifolia*; D, *H. sericea*; E, *E. grandis* and F, *P. pinaster*.

Discussion

The research undertaken in this chapter has demonstrated that it is possible to rank invasive perennial species according to their individual threat to the natural environment in an agricultural area by analyzing distribution density and population structure data. Analyses of these data also allow major invaders to be distinguished from emerging invaders.

Nel *et al.* (2004) categorise 'major invaders' as those invasive alien species that are well-established invaders, and which already have substantial impact on natural and semi-natural ecosystems. They suggest that another category of invaders, termed 'emerging invaders', currently have less effect, but have characteristics and potentially suitable habitat that could result in extended range and significance in the next few. Major invaders are arranged into groups based on geographic range and abundance, while emerging invaders are grouped based on current propagule-pool size and potentially invasive habitat (Nel *et al.* 2004). They add that 'emerging invaders' are currently afforded lower priority in management, but that it is conceivable that some of these species could become more important in the furture. These species may be targets for pre-emptive action (such as biocontrol) and they should be carefully monitored to guarantee that they do not become significant problems (Nel *et al.* 2004).

The factors that we considered in ranking the six study species in terms of their threat to natural ecosystems and water yields at De Rust are based on distribution and population structure data. When individuals of species have high growth rates, reach reproductive maturity in a short period under a wide range of environmental conditions and have the ability to disperse propagules to new sites suitable for establishment and growth, they are likely to pose a greater threat of invasion (Baker 1965,1974; Newsome and Noble 1986; Kolar and Lodge 2001). For a species to be considered a 'major invader' and difficult to remove, it would have to be abundant and widespread throughout the farm. Its presence would consume a considerable percentage of the farm area and its population age structure would reflect a large reproductive potential. This would mean that the restoration process could take longer and allow the chance of reinvasion from uncleared areas. A species poses a threat of further invasion if it can resprout from rootstock after clearing, spread from continuing long distance dispersal (saltation dispersal) and from short distance dispersal (diffusion dipersal) with lateral expansion of the established population (Smith *et al.* 1999; Davis and Thompson 2000). The threat posed to the natural environment by an invasive species was therefore considered as a combination of the potential for spread, or 'threat of invasion', and its abundance and distribution, or 'difficulty of removal'. 'Emerging invaders' were distinguished from 'major invaders' according to the characteristics mentioned by Nel *et al.* (2004).

Black wattle (*Acacia mearnsii*), white and grey poplars (*Populus alba; P. canescens*) and mesquite (*Prosopis glandulosa* var. *torreyana/velutina*) are the three species-groups falling within the 'very widespread-abundant' category of the SAPIA (Southern African Plant Invaders Atlas) ranking system created by Nel *et al.* (2004). Their study found that the Working for Water programme has allocated more funds to the regulation of black wattle than all other invasive alien plants together. According to distribution and population age structure data that were collected, the greatest threat to the natural environment at De Rust is likely to be *A. saligna* and *A. mearnsii*. They are predominantly found growing together and their distribution (difficulty of removal) represents the second largest total area of the species considered in the study. Population age structures also suggest that their reproductive potentials (threat of invasion) are greatest (*A. saligna*) and 3rd greatest (*A. mearnsii*). This could be due, at least partly, to the fact that their biological control agents, *Uromycladium tepperianum* (Sacc.) McAlp for *A. saligna* (Morris 1999) and *Melanterius maculatus* Lea for *A. mearnsii* (Dennill *et al. 1999*), are absent on the farm (*pers. obs.*). Therefore, growth and seed production are not currenlty limited. In addition, these species can reach reproductive maturity quickly, within 4 to 5 years, relative to the other species (New 1984). These species could therefore be considered as 'major invaders'.

Pinus pinaster poses the third greatest threat to the natural environment at De Rust. It is present in the greatest total area of all the invasive species and would therefore require a labour intensive clearing programme to remove the species from the farm. A study by Rouget *et al.* (2004) has shown that isolated pine trees can establish in undisturbed native plant communities. Fortunately, at present only 30% of the population is capable of reproduction and the remaining seedlings and saplings would take up to 10 years to reach maturity (Agee 1998). This means that the spread of the species can be controlled in a fairly simple manner if control procedures are implemented in the short-term. Another positive aspect of the large percentage of saplings in the population is that there is the potential to help fund the clearing programme if they are harvested and sold during December when a market for Christmas trees exists. Macdonald (2004) agrees that the use of the biomass (mainly wood) generated by the primary clearance of dense infestations of well-established invasive alien trees such as pines, gums and wattles, can establish secondary industries and go a long way towards funding the initial costs clearance. However, he warns that there are few benefits to be gained from such secondary industries in the subsequent clearing operations and rehabilitation of habitats, which invariably constitute the majority of the work in manual clearing.

The species that poses the fourth greatest threat is *H. sericea.* This is again possibly because its biological control agent, a seed-feeding weevil *Erytenna consputa* Pascoe (Gordon 1999), is not present in the population. The species has a short juvenile period and can produce seed within 2 years (Richardson 1987). The population age structure shows that there are many adult plants that have recently reached reproductive maturity and have the potential to produce a large seed bank in the next few years. This may qualify the species to be considered an emerging invader at De Rust. The largest population of this species covers a hilltop in a remote corner of the farm, where roads have been abandoned since 1996 (Dr. Cluver *pers. Comm.*) therefore, tt is likely that few people visit the area to check the state of the invasion. It possible that the species could be overlooked during the planning of clearing programmes. The species is also characterized by its spiney leaves, which make it difficult to work with. Special equipment is necessary for workers to avoid injury (Croudace 1999), therefore it may have been avoided during previous clearing initiatives. The minimum average rainfall over the natural distribution of *H. sericea* is 600mm (te Roller, 2004). It is therefore possible that it can be restricted to relatively drier slopes and hilltops where it is able to dominate over species with higher moisture requirements, while being outcompeted by more aggressive invaders, such as *A. mearnsii* and *A. saligna*, in and around watercourses. However, the species is absent from almost all hilltops near to areas of agricultural activity and those areas that have experienced any vegetation management, for example brush cutting or mowing.

The fifth greatest threat at De Rust is *E. grandis.* The population age structure suggests that the species produces more seedlings than *A. longifolia* and *H. sericea.* Therefore, population spread could occur if enough time is allowed for those seedlings to reach maturity. Fortunately, the species requires relatively longer periods to do this as the most common age for the start of seed production in any significant quantity is between 20 and 40 years (Jacobs 1955). This, in combination with the small area of invasion, implies that control of spread is relatively easy.

Acacia longifolia poses the smallest threat to the natural environment at De Rust, even though it is present in the largest amount of area after *A. saligna*, *A. mearnsii* and *P. pinaster*. The reproductive output of the population is low, evident in the low numbers of seedlings in the population age structure. This is most likely due to the presence of its biological control agent, the bud-galling wasp *Trichilogaster acaciaelongifoliae* Froggatt (Dennill *et al.* 1999). This means that the spread of the species has been reduced to a rate that allows removal without the potential for major reinvasion.

The combination of invasion risk and removal difficulty to rank alien species in terms of their threat to endemic ecosystems requires knowledge of the distribution, abundance, population structures, biological control agents and life histories of the species concerned as well as the ability to operate a geographical information system and manage a large database. These factors showed that *A. saligna* and *A. mearnsii* are major invaders and collectively pose the greatest threat to the environment at De Rust. This type of study could also be suitable for small nature reserves where conservation of natural vegetation is essential. However, this method of determining invasion risk could become impractical if the study area was too large or contained very few roads. This would mean that the amount of time spent travelling between study sites and domestic facilities could become a sizable limiting factor on the amount of data that can be collected on a particular day. Farm labourers could possibly be used to collect data if special training was provided, but only a specialist could analyse the dataset. Further study could be conducted on the relationship between land-use type, topography and invasive species in order to model the potential density of future invasions in an agricultural landscape.

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CHAPTER 3

Invasive perennial weeds associated with different land-use categories in an agricultural area of the Western Cape Province.

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Introduction

According to the distribution data in the SAPIA (Southern African Plant Invaders Atlas) database (Henderson 1998), reported in Nel *et al.* (2004), almost 80% of the grid-cells within South Africa presently contain invasive alien species and nearly 35% support 10 or more species. These grid cells correspond to areas with a high proportion of transformed land (such as agriculture, forestry and urbanization), high rainfall and a high population density (Nel *et al.* 2004). Latimer *et al.* (2004) calculated that human land-use and invasive alien plants have transformed almost a third of the area of the CFR (Cape Floristic Region). The characteristically more fertile soils of renosterveld in the CFR have resulted in large areas being transformed for the cultivation of wheat (Rebelo 1995). For example, only 4% of the original area of West Coast renosterveld remains unaltered (Rebelo 1995). The conservation status of this vegetation is very poor, and less than 1% is officially protected (Rebelo 1995). Rouget and Richardson (2003) found that almost the entire Agulhas plain, which contains large areas of transformed renosterveld, has been invaded by woody alien plants to some extent. They state that alien species occur in 72% of the total area and 96% of the remaining vegetation (cultivated and urbanized areas excluded).

Richardson *et al.* (2004) report an alarming revelation that various elements of global change, for example global warming, elevated atmospheric CO_2, nitrogen deposition and habitat fragmentation, are interacting to amplify the impacts of plant invasions. Richardson and van Wilgen (2004) add that such invasions are likely to be influenced by climate change (Richardson *et al.* 2000) in many parts of the country (Milton 2004). Altered climate patterns could have significant consequences for the distribution of alien plant species (Richardson *et al.* 2000). This is because habitat boundaries are expected to shift to higher altitudes (Benning *et al.* 2002). Therefore, some alien species that are currently non-invasive or only naturalized and/or which persist as isolated populations could become (more) invasive as climate changes. Due to the uncertainty of the effects of climate change on plant invasions, Rouget *et al.*

(2004) stress the importance of including climatic factors in simulation models of invasive species spread.

A relatively new method of research in the field of invasive plants is the computerised simulation model (Richardson *et al.* 2000; Shafii *et al.* 2003; Rouget *et al.* 2004). Such models rely on mathematical relationships between invasive plants and the environment to predict outcomes of alien plant presence in landscapes. Predictions can be made at various scales, depending on the nature of the data that derived the mathematical relationships forming the basis of the simulation. Richardson and van Wilgen (2004) propose that data on the geographical distribution of invasive alien plant species only provides information at one level and that it is critical to know how abundant or dense invasive species can become at finer scales. However, Gorgens and van Wilgen (2004) warn that researchers face the problem of scaling up from site-specific observations. It is wise to bear this warning in mind, because spatial patterns of invasion result from many diverse interacting factors, including biological attributes of the invader, species response to the abiotic environment, biotic interactions and human activities (Richardson *et al.* 2004).

Richardson and van Wilgen (2004) propose that there is a scarcity of well-documented accounts of the impacts of invasions, and of robust models enabling us to scale-up our predictions of results on the delivery of ecosystem goods and services. The development of that kind of model demands a better understanding of the results of invasions at fine scales. They advise caution because outcomes can vary with species, soil type and disturbance regime, and thus further complicate the task. Improved understanding of the process of invasions would require including changes in land-use and habitat fragmentation in simulation models (Rouget *et al.* 2004). Predictions at the landscape or regional scale could be improved by quantifying more rigorously the aspects of disturbance regimes and the spatial structure of landscapes (Rouget and Richardson 2003). For this reason, our study aims to provide evidence that a relationship exists between land-use type and invasive plant species density, at a relatively fine scale, in an agricultural environment within the renosterveld and fynbos biomes of the Cape Floristic Region. Our data also allows us to identify which perennial invasive species presents the greatest threat to conservation of remnant patches in agricultural areas, by using De Rust Estate (Elgin Valley, Western Cape Province, South Africa) as a case study. We propose that relationships between land-use and perennial invasive species could support and supplement simulation models of alien plant invasion in agricultural areas of the Cape Floristic Region.

Methods

Site description:

De Rust is a farm situated in the Elgin valley, near Grabouw in the Western Cape Province, South Africa. The 2600 ha property is situated on the foothills of the Groenlandberg mountain range (19.10° E; -34.16° S) and contains an altitudinal gradient stretching from the lower mountain slopes (around 600 m above sea level) towards the drainage basin in the valley bottom (around 250 m above sea level). The natural vegetation in the area is described by the C.A.P.E. project as Elgin Fynbos/Renosterveld Mosaic, which is essentially Renosterveld with many Fynbos elements (Helme 2003). The agricultural activities undertaken on the property include vineyard and orchard cultivation, as well as small-scale livestock and game rearing. The majority of the property (1600 ha) was included in this study, and only the area on the southern side of the N2 highway, as well as some of the uninvaded steeper slopes of the Groenlandberg property border and were excluded.

The six most common invasive perennials within the De Rust property boundaries were selected for the analysis of possible statistical relationships with land-use types. These species were identified as the most abundant and widespread in a pilot survey of the farm. A handheld GPS receiver was then used to identify the location of stands of *Acacia saligna* (Labill.) H.L.Wendl., *A. mearnsii* (De Wild.), *A. longifolia* (Andr.) Willd. *Mimosaceae, Hakea sericea* Schrad. & J.C.Wendl. *Proteaceae, Eucalyptus grandis* W. Hill ex Maiden *Myrtaceae* and *Pinus pinaster* Aiton *Pinaceae* plants. Transects were walked along stand edges so that co-ordinates of data points, separated by between 50m and 100m, could be sampled. At each datat point, the presence/absence, as well as the density, height and stage of each of the 6 chosen species was estimated. Land-use type was also recorded at each datapoint. Transects were structured in such a way that nearly all stands of the six chosen species could be included in the study and so that data from different land-use types could be separated from each other during data analysis. Further transects were walked along major roads and across land-units between roads.

Land-use categories were classified according to the activities undertaken at the area concerned. There were originally 16 categories that described specific differences between land-uses, these were: Road verge, old road, remnant patches of indigenous vegetation, undisturbed remnant patches of indigenous vegetation, windbreak, old windbreak, vineyard, orchard, dam edge, dam wall, river, forest, forest edge, railway line, property edge and airfield. Some of these categories were identified to describe the same broad land-use types and were therefore merged so that eight general land-use categories were created. Road verges were areas directly adjacent to existing roads as well as areas that had been used as roads in the past and had since been abandoned. Remnant patches were fields that had never been, or were not at the time of data collection, used for agricultural of arboricultural practices. However, game and livestock rearing camps were included under the remnant patches category even though they could be considered as a form of agricultural practice. Nonetheless, the vegetation of these camps was dominantly indigenous. Windbreaks and old windbreaks were narrow areas bordering orchards, vineyards and some property edges that contained adult trees or stumps of felled adult trees, usually *Pinus* species, but in some cases *Eucalyptus* or *Populus* species. The category vineyards and orchards refers to areas in the very nearby vicinity of vineyards and orchards as no alien plants were found growing in vineyards and orchards themselves, but some alien plants were encountered near to the borders of vineyards and orchards. The dam category includes areas bordering any part of a dam, including the steep slope of the dam wall. Rivers were defined as riparian zones within and around drainage lines, including perennial and ephemeral rivers. Forests were defined as areas within, and directly adjacent to, dense stands of adult trees that formed a closed canopy over an area of at least 100 m². Railway lines were defined as areas directly adjacent to train tracks. Property edges were areas where De Rust bordered with neighbouring properties. The fact that railway lines are areas that are not owned and managed by De Rust Estate warranted the merger of the property edge and railway line categories. The light aircraft landing strip was a small area that defined the airfield category and the data collected from this area was included in the railway line/property edge land-use category.

Stand density was separated into four categories. ‘Sparse’ refers to areas where less than 5 individuals of a species were present. ‘Intermediate’ describes stands of between 5 and 20 individuals of a species. ‘Dense’ areas contained more than 20 individuals of a species and to classify an area as ‘Very dense’ meant that the stand was so dense that a person could not walk, or even see more than a few metres, into the area.

Population structure of invasive perennials

The life stage structure of each species was recorded in four categories. ‘Seedling’ refers to small plants (less than 20 cm tall) that have recently germinated. ‘Sapling’ means young plants that had not reached reproductive maturity. ‘Adult(s)’ were established plants that did not show any signs of flowering or seed production and 'flowering adults' defined established plants that were in the process of producing flowers or seeds or on which there was evidence of old flowerheads. Stage categories were broadly structured so that they could also provide a rough approximation of plant age. The difference between life stage and the age of plants in that stage is a qualitative measure of a plants position in its life history cycle, while age is the quantitative measure of how long a plant has lived. Stage category frequency is therefore a rough representation of the population age structures of the selected invasive species at De Rust.

The heights of plants were recorded in seven categories. Areas classified as '<1m' meant that all plants were shorter than 1 m in height. Similarly, '<2m' refers to areas where all plants were shorter than 2 m in height. This type of classification was applied to areas where all plants were shorter than 3 m ('<3m'), 4 m ('<4m') and 5 m ('<5m') in height. When all plants were taller than 5 m, the area was assigned to the '>5m' category. The final category was '1 - >5m' and defined areas where plants were found in a range of heights from 1 m to greater than 5 m tall. Height category frequency is a measure of stand maturity, or the length of time that a stand has been present in the landscape

Relationship between land-use and invasive species

The number of records (frequency) of each species in all land-use categories was totaled. The percentage of records found in each land-use category was then displayed as species specific histograms.

Relationship between land-use and stand density, height and stage categories

The number of records (frequency) of a species found in each density, height and stage category was summed separately. These totals were the observed frequencies of density, height and stage categories for each species in each land-use category respectively. These contingency tables were used to calculate the expected frequency within each category and to compare observed *vs.* expected frequencies in a log-likelihood ratio test (a variation of the χ^2 analysis described in Bliss 1967; Sokal and Rohlf 1969; Zar 1974). The resulting log-likelihood ratio tables are displayed in Appendix C.

The log-likelihood ratio method is a test similar to the χ^2 analysis. It is applicable and preferred over the standard χ^2 analysis when some cells of the observed frequency table contain a zero value (Bliss 1967; Sokal and Rohlf 1969; Zar 1974). The formula used to calculate the cells of the log-likelihood ratio table (μ_{ab}) is:

$$\mu = 2O_{ab}.\ln(O_{ab}/E_{ab})$$

where μ is the specific log-likelihood ratio cell value in row a, column b; O is the observed frequency in row a, column b and E is the expected frequency in row a, column b (Zar 1974). The cells in the resulting log-likelihood ratio table (μ_{ab}) are summed to yield the log-likelihood ratio statistic (χ^2). This value is the equivalent of the result from a Pearson χ^2 analysis and allows the calculation of a P-value in the same way as in a standard χ^2 analysis. The level of statistical significance of the resulting log-likelihood ratio statistic (χ^2) is defined as:

$$P > \chi^2_{(a-1)(b-1);\ \alpha}$$

where P is statistically significant at the critical level (α) if its value is greater that the Chi square statistic with (a-1)(b-1) degrees of freedom. Analysis of the individual cells in the log-likelihood ratio table highlights which cells contributed the greatest amount to the final log-likelihood ratio statistic (χ^2), and therefore the P-value or degree of statistical significance. If each species contributed equally to the level of significance, then their cell values would be approximately 1/6th of the final log-likelihood ratio statistic (χ^2) value. Therefore, in order to identify cell values that made greater than expected contributions to the χ^2 value, special attention was given to positive cell values greater than 1/5th of the χ^2 value. The land-use category is most highly correlated with specific density, height or stage categories at these cells. For example, areas with tall trees, like windbreaks, should have high χ^2 values in height categories such as >5 m. This would demonstrate that it was most likely for tall trees to be observed at that land-use type. Conversely, negative cell values that were greater than 1/5th of the χ^2 value were also noted. These values demonstrate which density, height or stage categories are most unlikely at each land-use type.

Cartography

Maps depicting land-use were created using ArcView 3.2 and the GPS referenced data collected at De Rust Estate. Three separate maps were created (1) a map of all eight land-use categories (Appendix D, Figure 1), (2) a map depicting the road network, the railway line, the airstrip, remnant patches and remnant patches that had recently been cleared of all vegetation, including alien and indigenous and (Appendix D, Figure 2)

(3) a map displaying the road network, the railway line, the airstrip, forests, vineyards and orchards (Appendix D, Figure 3). The first map was used to calculate the percentage of De Rust Estate land within each land-use category. The second map was created to show the extent of current invasive woody perennial clearing activities. The third map was created to show patches of land dedicated to agricultural activities.

Results

The specific frequency of records in each land-use category (Figure 2.1) shows that all species were most frequently (>75%) found in remnant patches. The second most frequent (>47.6%) land-use category for all species except *A. saligna* was 'Road verge' (Figure 2.1). *Eucalyptus grandis* had the greatest percentage (66.6%, n=296) of individuals growing in the 'Road verge' category (Figure 2.1). The second most frequent (44.2%, n=737) land-use category for *Acacia saligna* was 'River' (Figure 2.1). The least frequent (<18.9%) categories were 'Dam', 'Forest' and 'Vineyard/Orchard' (Figure 2.1).

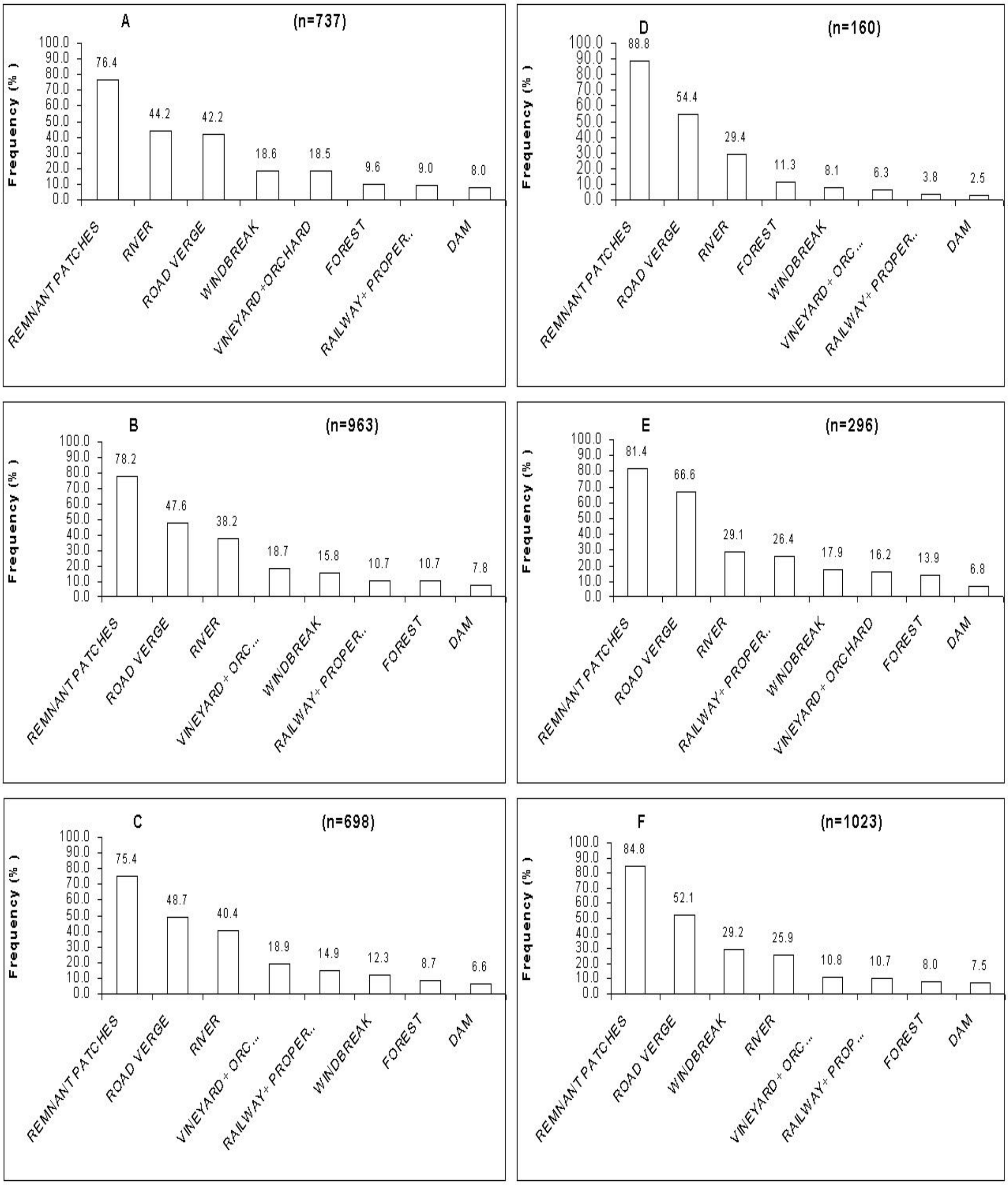

Figure 3.1. Percentage frequency of species in the different land-use categories; A, *Acacia saligna*; B, *Acacia mearnsii*; C, *Acacia longifolia*; D, *Hakea sericea*; E, *Eucalyptus grandis*; F, *Pinus*

The log-likelihood ratio tables demonstrate that the relationships between land-use and density, height and age for certain species were highly significant ($P<0.01$; P-values range between 1.35×10^{-3} and 2.7×10^{-224}). The log-likelihood ratio tables of land-use *vs.* density categories (Appendix C) are summarised in Table 3.1 which highlights the land-use categories that added >20% of the total log-likelihood ratio statistic for each species. Table 3.1 shows that, for the majority of species considered individually, sparse stands were encountered at greater than expected frequencies along road verges, while stands of intermediate density were encountered at greater than expected frequencies in remnant patches. 'Dense' stands were more frequent than expected in rivers and forests, while very dense stands were more frequent than expected in remnant patches and rivers (Table 3.1). The 'ALL' value shows that, when all species were considered together, dams, vineyards/orchards and road verges were associated with sparse stands more frequently than expected, windbreaks with intermediate stands, remnant patches with intermediate and very dense stands, forests with dense stands and rivers with dense and very dense stands (Table 3.1). The 'ALL' value does not occur in the railway line/property edge land-use category, suggesting that species frequency was distributed fairly evenly throughout the four density classes in this land-use category. However, it is clear that *E. grandis* and *A. longifolia* were found in very dense stands adjacent to railway lines or at property edges more frequently than expected if one considers these species individually.

Table 3.2 highlights the land-use categories that subtracted >20% of the total log-likelihood ratio statistic for each species. The case for the majority of species, when considered individually, was that sparse and intermediate stands were encountered less frequently than expected in rivers, while dense stands were less frequent than expected in remnant patches and along road verges. The latter was also the land-use category encountered less frequently than expected for very dense stands. The 'ALL' value shows that, when all species were considered together, rivers were infrequently associated with sparse and intermediate stands, windbreaks with sparse and dense stands and forests with intermediate stands. Remnant patches and road verges were infrequently associated with dense stands. The 'ALL' value does not occur in vineyards/orchards and dams, suggesting that there was a relatively even distribution of density class frequency in these land-use categories.

The log-likelihood ratio tables of land-use *vs.* height categories (Appendix C) are summarised in Table 3.1. Land-use categories that represent >20% of the total log-likelihood ratio statistic for each species (Table 3.1) suggest that *H. sericea* was found growing more frequently than expected at heights of <3 m at road verges, rivers and remnant patches. Furthermore, it is clear that *P. pinaster* was found growing more frequently than expected at heights >5 m at road verges, windbreaks, vineyards/orchards, forests and railways/property edges (Table 3.1). *Acacia mearnsii* was encountered growing more frequently than expected at heights ranging from 1 m to >5 m at road verges, dams, rivers, remnant patches, vineyards/orchards and forests (Table 3.1). *Eucalyptus grandis* was encountered growing more frequently than expected at heights ranging from 1 m to >5 m at road verges and railways/property edges (Table 3.1). The only height frequency value >20% below expected was for *A. longifolia* growing at heights from 1 m to >5 m in rivers (Appendix C).

The log-likelihood ratio tables of land-use *vs.* stage categories (Appendix C) are summarised in Table 3.1. Land-use categories that represent >20% of the total Log-likelihood ratio statistic for each species (Table 3.1) suggest that *A. saligna* saplings were more frequent than expected in rivers. Adult *A. longifolia* plants were more frequent than expected at road verges, dams, rivers, remnant patches and vinyards/orchards, while adult *P. pinaster* plants were more frequent than expected in windbreaks (Table 3.1). *Eucalyptus grandis* sapling and adults were found growing together more frequently than expected at railways/property edges. In the case of *A. mearnsii*, more saplings and flowering adults than expected were found growing together at rivers, road verges and remnant patches. Furthermore, greater frequencies of *A. mearnsii* seedlings, saplings and flowering adults than expected were found growing together at rivers, vineyards/orchards and forests.

Table 3.1. Summary of respective land-use *vs.* density, height and stage log-likelihood ratio values that contributed >20% to the log-likelihood ratio statistic. AS, *Acacia saligna*; AM, *Acacia mearnsii*; AL, *Acacia longifolia*; HS, *Hakea sericea*; EG, *Eucalyptus grandis*; PP, *Pinus pinaster*

Land-use	Most common density	Height and species	Stage and species
Road	Sparse	<3m HS >5m PP 1->5m AM & EG	Adult AL Sapling & flowering adult AM
Remnant patches	Intermediate	<3m HS 1->5m AM	Adult AL Sapling & flowering adult AM
River	Dense; Very dense	<3m HS 1->5m AM	Sapling AS Adult AL Sapling & flowering adult AM Seedling, sapling & flowering adult AM
Forest	Dense	>5m PP 1->5m AM	Seedling, sapling & adult AM
Dam	Sparse	1->5m AM	Adult AL
Windbreak	Intermediate	>5m PP	Adult PP
Vineyard/ Orchard	Sparse	>5m PP 1->5m AM	Adult AL Seedling, sapling & flowering adult AM
Railway/ Property edge	None	1->5m EG >5m PP	Sapling & adult EG

Table 3.2. Density categories subtracting >20% of total log-likelihood ratio statistic for each species in each land-use category. AS, *Acacia saligna*; AM, *Acacia mearnsii*; AL, *Acacia longifolia*; HS, *Hakea sericea*; EG, *Eucalyptus grandis*; ALL, all 6 species combined

Land-use category	Sparse	Intermediate	Dense	Very dense
Remnant patches	AL;HS		AS;EG; ALL	
Road		AL;HS	AS;AM; ALL	AS;AM
River	AS;AM;AL; ALL	AS;AM; ALL		
Windbreak	ALL		AL; ALL	
Vineyard/orchard				
Railway/property edge		AL;EG		
Forest		ALL		
Dam				

Cartography

ArcView analysis of maps dividing De Rust Estate into separate land-use categories yielded measures of total area, and the percentage of farm area, devoted to each land-use category. Clearing activities currently occupy 1.7%, while economic activities are present in 15.2% of De Rust Estate (Table 3.3). The total length of the road network was roughly calculated as 63km. It was also calculated that 5.5km of railway line runs over De Rust Estate land.

Table 3.3. Total area (km^2) and percentage of farm area in each land-use category.

Land-use category	Area (km^2)	Percentage of farm area
Remnant patches	8.11	48.41
Vineyard/Orchard	2.55	15.22
Forests	2.20	13.15
Rivers	1.72	10.26
Dams	0.56	3.36
Cleared remnant patches	0.29	1.70

Discussion

The research undertaken in this chapter demonstrates that statistically significant relationships exist between some land-use categories and the density, and certain aspects of the population structure, of some invasive perennial species. These findings could contribute to the accuracy of simulation models of invasive plant species distribution and spread, at a relatively fine scale, in agricultural areas.

Roads

Vila and Pujadas (2001) performed a stepwise regression analysis between several land-use and socio-economic parameters and the density of alien species in European and North African countries. They discovered that the extent of terrestrial transport networks and the percentage of protected areas were the land-use variables that best accounted for the density of alien plants at the scale of whole countries. Roads, in an agricultural setting, border several other land-use categories such as windbreaks, vineyards/orchards, dams and plantation forests. One could expect tall pine and eucalypt trees to be more common than the other study species along roadsides due to the presence of deliberately planted windbreaks and plantation forests. Theoretically, transport networks enhance immigration rates of new species and the spread of exisiting ones (Ernst 1998). Areas adjacent to roads have been found to support high numbers of alien species at the regional scale, even within nature reserves (Tyser and Worley 1992; Pysek 1994). The fact that invasive plants commonly occur in sparse stands along roads shows that, at De Rust, alien plant control has occurred in these areas. These areas may be targets for clearing initiatives for several reasons. Accessibility to the clearing site, on foot, or by motor vehicle may influence site selection. Transport arteries could allow anyone to identify stands of invasive plants without disturbing the natural vegetation or exposing the observer to fatigue or danger from venomous snakes or parasitic insects such as ticks.

Rouget *et al.* (2004) found that pines were invading natural vegetation in the lowlands of their study site where agriculture and other human activities had fragmented natural vegetation. These remnants of natural vegetation were predominantly privately owned, and are considered high priorities for conservation (Kemper *et al.* 1999, 2000. The reasons why *A. mearnsii, A. longifolia* and *H. sericea* are the most common invasive species in these areas at De Rust are speculative. Tall *Acacia mearnsii* trees are commonly used as shade trees for farm labourers in areas near to orchards or vineyards. Rouget *et al.* (2004) found that in their study area, pines were intentionally moved around the area by humans and planted for different purposes, including the provision of shade or aesthetics. Tall *Acacia mearnsii* trees areas allow labourers cooler temperatures during lunch breaks and could therefore be seen as desirable in the landscape. A large area in a remote corner of De Rust estate is covered by *H. sericea*, this area is removed from the road network and its inaccessibility could explain why clearing has not taken place. Very large remnant patches without a suitable transport route to allow easy access to the invaded areas could therefore be prone to invasion from neighbouring areas, because it may be difficult to observe invasive species during the early stages of invasion.

Rivers

Riparian zones found in drainage networks are important landscape units (Malanson 1993). Riparian vegetation governs the flow of water, nutrients and sediments into streams (Forman and Godron 1986; Junk *et al.* 1989); it serves as a landscape corridor which facilitates the movement of organisms (Forman and Godron 1986; DeFerrari and Naiman 1994); it generally, but not necessarily in fynbos, contains disproportionately high species richness (Murray and Stauffer 1995). Regular floods might allow the high plant species richness of riparian zones because they reduce the strength of competitive interactions, periodically return portions of riparian community to early successional stages, and create a complex and shifting mosaic of landforms that provides a diversity of microhabitats (Gregory *et al.* 1991; Decamps and Tabacchi 1992; Pollock *et al.* 1998). However, the same factors may also increase susceptibility to invasion by exotic species (Pysek and Prach 1994). In addition, the availability of moisture and the dispersal of propagules by water may be alternative or synergistic causes of the invasibility of riparian zones (Hood and Naiman 2000).

Theoretically, the high plant species richness of riparian systems should reduce their invasibility because communities comprised of many strongly interacting species are thought to restrict the invasion possibilities of most similar species (Pimm 1989; Case 1990). Planty-Tabacchi *et al.* (1996) found that, contrary to theoretical predictions, species richness was positively correlated with the proportion of exotic species as one moved from the headwaters to the lower courses of both the Adour River in southwestern France and the McKenzie River in northwestern USA. Hood and Naiman (2000) theorize that species richness could be important in reducing the invasibility of undisturbed communities and not in communities experiencing frequent disturbance. However, the streams at De Rust represent riparian zones with arguably infrequent disturbance. This is assumed, due to the absence of evidence of flooding and the narrowness of stream channels. It is also likely that the network of dams restricts the natural flood pulses that would occur in undammed rivers. Riparian areas are some of the most densely invaded areas on the farm and we theorize that this is due to the high moisture requirements of some of the selected study species. This would result in these species displaying a preference for areas with greater amounts of available water. Hood and Naiman (2000) compared the vulnerability of riparian plant communities high on river banks with those on floodplain floors and found that floors have 3.1 times more exotic plants than banks. However, their study was conducted on mixed bedrock-alluvial macro-channels in the Kruger National Park, which are distinctly different when compared to the streams found at De Rust. Nonetheless, they concluded that macro-channel floor regions of the riparian zones of South African rivers are highly vulnerable to invasion by exotic vascular plants. The streams at De Rust have banks, but no floodplain floors associated with macro-channels. Therefore areas that can be considered as stream banks contain the greatest densities exotic plants in riparian areas at De Rust. As the distance from the stream increases there is a change in the vegetation, which corresponds to a gradient of declining riverine influence on the exotic vegetation and is analagous with the findings of van Niekerk and Heritage (1993).

Research to date has established that tall alien trees, such as pines, eucalypts and wattles, generally diminish total annual and low-season streamflow (Bosch and Hewlett 1982; Scott *et al.* 2000; Dye and Jarmain 2004), and increase evapotranspiration (Dye *et al.* 1997) compared to the indigenous vegetation that they replace. Decreases in the long-term mean annual runoff have been in the order of 100-300 mm/yr, but all the experimental catchments on which conclusions were based were in high rainfall zones (>1100mm/yr). Water use by specific invasive alien plant species is dependant on leaf area of the plants (which correlates roughly with age and biomass), but water use by different invasive alien plant species in the same environment can vary considerably (Gorgens and van Wilgen 2004). After clearing of dense and extensive stands of alien trees, it may take several years before stream flow recovery approaches pre-planting levels (Van Lill *et al.* 1980), indicating that soil water resources can be depleted and need replenishment (Dye and Bosch 1999). Evapotranspiration by riparian alien woody plant communities is noticeably greater than by indigenous plant communities in the same setting (Dye *et al.* 2001). Experimental clearing of riparian zone invasives during the low-flow season has lead to significant stream flow increases in both winter and summer rainfall regions, with estimates ranging from 9 to 31 cubic meters per day per ha cleared (Dye and Poulter 1995; Prinsloo and Scott 1999; Rowntree and Beyers 1999). Therefore, it is possible that invasive plants at De Rust have used up a substantial amount of water that would have ended up in dams.

Forests

During the 1860s, eucalypts and pines were planted in groves near to Grahamstown in the Eastern Cape Province. A reduction in stream flow from the catchment containing these groves was noticed by 1909. The water had been used during the rapid growth and spread of these fast growing alien tree species in the catchment. (Macdonald, 2004). Many species form closed-canopy stands in some ecosystems. These include pines and hakeas in fynbos, as well as wattles (especially *Acacia mearnsii*), eucalypts and giant reed (*Arundo donax*) along rivers (Richardson and van Wilgen 2004). In our study, Forests, or groves, were defined as areas >100 m^2 that contained dense stands of adult trees forming a closed-canopy. Plantation forests of *P. pinaster* were most common at De Rust Estate, but dense stands of *A. mearnsii* were also common enough to be classified as forests. The dense invasions of *A. mearnsii* were likely to be within remnant patches where multiple combinations of stage classes, from seedling to adult, were present in significant quantities, but were so large that they were considered as forests on their own. The presence of these forests could have reduced stream flow to some extent since the time that they were planted. Their presence could also have facilitated invasion of neighbouring areas as they may have provided as source of propagules to permit such invasions.

Dams

There is no literature dedicated to the study of invasive plants and dams, but one could expect that dams are well looked after in general, as they are important for the supply of water for agricultural activities. Sparse stands of invasive species were most common at the dams within De Rust Estate and we propose that invasive plant clearing is likely to have occurred at these sites. The possibility of enhanced plant available water resources is increased near to dams, which could allow greater densities of invasive plants. These areas are also well connected to the road network, thus access and anthropogenic importance could be key factors in predicting areas that are cleared of invasive species most often and therefore contain mostly sparse stands of invasive species.

Windbreaks

In windbreaks, there was a distinct absence of any invasive species, other than *Pinus pinaster*, in any significant quantity. The narrow area that windbreaks occur in and their close proximity to the road network could make it easy to identify and remove invasive species before they reach reproductive maturity and cause further invasion. However, *Pinus pinaster* is one of the introduced species in South Africa that has radiated from sites of plantations and become known as an invasive perennial species (Richardson and Higgins 1998). Rouget *et al.* (2004) found some evidence that proximity to watercourses increases the probability of *P. pinaster* occurrence. Therefore, windbreaks could have served as sources of seeds for subsequent invasion of *P. pinaster*, especially near to riparian zones.

Vineyards and orchards

Sparse stands of invasive plants are most common around vineyards and orchards, suggesting that clearing activities could have taken place in these areas. The road network is focused on providing vehicular and pedestrian access to these areas. Even though roads are known to enhance immigration rates of alien species (Ernst 1998), the frequency of human activity can provide the opportunity to identify invasive plants and possible invasions before they spread or reach significant densities. This could be achived simply by human presence in these areas, as opposed to areas that are infrequently visited by humans due to the absence of economic activities at those sites. The most common invasive plants around vineyards and orchards were tall *P. pinaster* trees and a range of different sized *A. mearnsii* trees. The abundance of pines reflects the fact that windbreaks bordered most vineyards and orchards. The strong presence of *A. mearnsii* could be attributed to their desirability as shade trees, comparable to the pines mentioned by Rouget *et al.* (2004), and the proximity of some vineyards and orchards to riparian areas, which contained dense stands of *A. mearnsii*.

Railway lines and property edges

Railway lines represent terrestrial transport networks existing in agricultural areas that are not managed by the farm owner. They are known to enhance the immigration rates of new species and the spread of existing ones (Ernst 1998). Areas adjacent to railway lines have been found to be rich in alien species at the regional scale, even within nature reserves (Tyser and Worley 1992; Pysek 1994). It is conceivable that they provide the opportunity for invasive plants to remain in a landscape once clearing activities have removed invasives from the farm property. The potential for reinvasion of farm areas is therefore increased by the presence of railway lines that are not managed effectively and cleared of invasive plants regularly. We found that *Eucalyptus grandis* was more common along railway lines and the fact that saplings and adults were found together suggests that this species has the potential to spread its population to uninvaded areas bordering railway lines. A deliberately planted windbreak, either of *P. pinaster* or *E. grandis*, delimited most property edges at De Rust. These windbreaks contributed to the significant proportion of tall *P. pinaster* plants that characterized the combined railway line/property edge land-use category. It may be beneficial to treat these land-use types as separate entities during the construction of a simulation model that includes the relationship between land-use type and invasive species.

Results to be disregarded

Adult *Acacia longifolia* plants were statistically abundant in most land-use categories, unlike most other species (*Acacia mearnsii* excluded) which were statistically abundant in only one or two land-use categories. The significance of these results should be disregarded because this species is no longer a landscape invader (refer to Chapter 2 discussion). The reason for this is most likely to be the presence of a biological control agent that inhibits seed formation and thereby reduces the number of seedlings in the landscape. Macdonald (2004) highlighted the distinctive advantages of using seed-feeding insects to diminish the invasive nature of alien plants. He said that the benefits are greatest where sectors of the community wish to retain a ‘transformer alien species’ in cultivation for its beneficial characteristics. These are the so-called ‘conflict-of-interest’ alien species as typified by black wattle, *Acacia mearnsii* and jacaranda, *Jacaranda mimosifolia*. It is likely that the species was an aggressive invader before the introduction of the biocontrol agent, because significant quantities of adult plants were found in five out of the eight land-use categories. However, it is not likely that the invasion of *A. longifolia* will spread.

Conclusion

Richardson and van Wilgen (2004) documented that there are dense invasions in the mountains and lowlands and along all major river systems of South Africa (Richardson *et al.* 1997; Rouget *et al.* 2003). The prominent invaders are trees and shrubs in the genera *Acacia, Hakea,* and *Pinus*. Proof that these species are also important invaders in agricultural areas is provided by our study. We conclude that invasive alien plants are concentrated in areas removed from human activity at De Rust and suggest that on privately owned land, in the absence of a strategically planned alien plant clearing initiative, invasive plants are removed where people observe them easily during a normal working days activity. This would result in clearing activities being initiated in areas that are subject to greater amounts of human traffic. Nel *et al.* (2004) contemplate that less methodical attention has been directed at categorizing invasive alien species already in a region to help draft regional or national plans for managing invasions. This could also be true for private land, the owners of which may be lacking the funding for such detailed scientific investigation. In such areas, limited resources force owners to make choices about where to focus control efforts, and which species to select for control (Nel *et al.* 2004). Gorgens and van Wilgen (2004) emphasize that existing knowledge needs to be used more efficiently, to help prioritize clearing procedures by targeting regions in terms of water-related benefits. Richardson and van Wilgen (2004) highlight that we require improved understanding of how to manage ecosystem recovery. They stress that this is especially critical for riparian systems, which are usually densely invaded, and subject to erosion after clearing. We suggest that farm owners, wishing to safeguard the integrity of remnant patches and avoid reinvasion of cleared areas, should perform a survey of invasive plants over their entire property and plan clearing projects systematically to deal with the greatest threats of invasion. Areas within a property that are managed by a separate entity should be identified as providing the possibility of reinvasion once clearing activities have taken place. The managers of such areas should be contacted and given the option of compensating the farm owner for clearing the invasive plants with his private labour force. Alternatively, managers could clear the area as they see fit and as is required by the Conservation of Agricultural Resources Act (Act No 43 of 1984).

The results presented in this project demonstrate the potential to include land-use categories into simulation models of invasive species spread. Even if our approach is only a statistical survey, it emphasises the need to determine the links between plant invasions and human activities. Further investigation could be conducted to determine scale to which these results could be extrapolated and this could be achieved by performing similar studies in other agricultural areas. Subsequent investigations could therefore lead to the detailed determination of the mathematical relationship between land-use categories and invasive plant species density which could enhance our ability to predict alien plant densities in agricultural areas.

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APPENDIX A: BUFFER AND POLYGON AREA MAPS

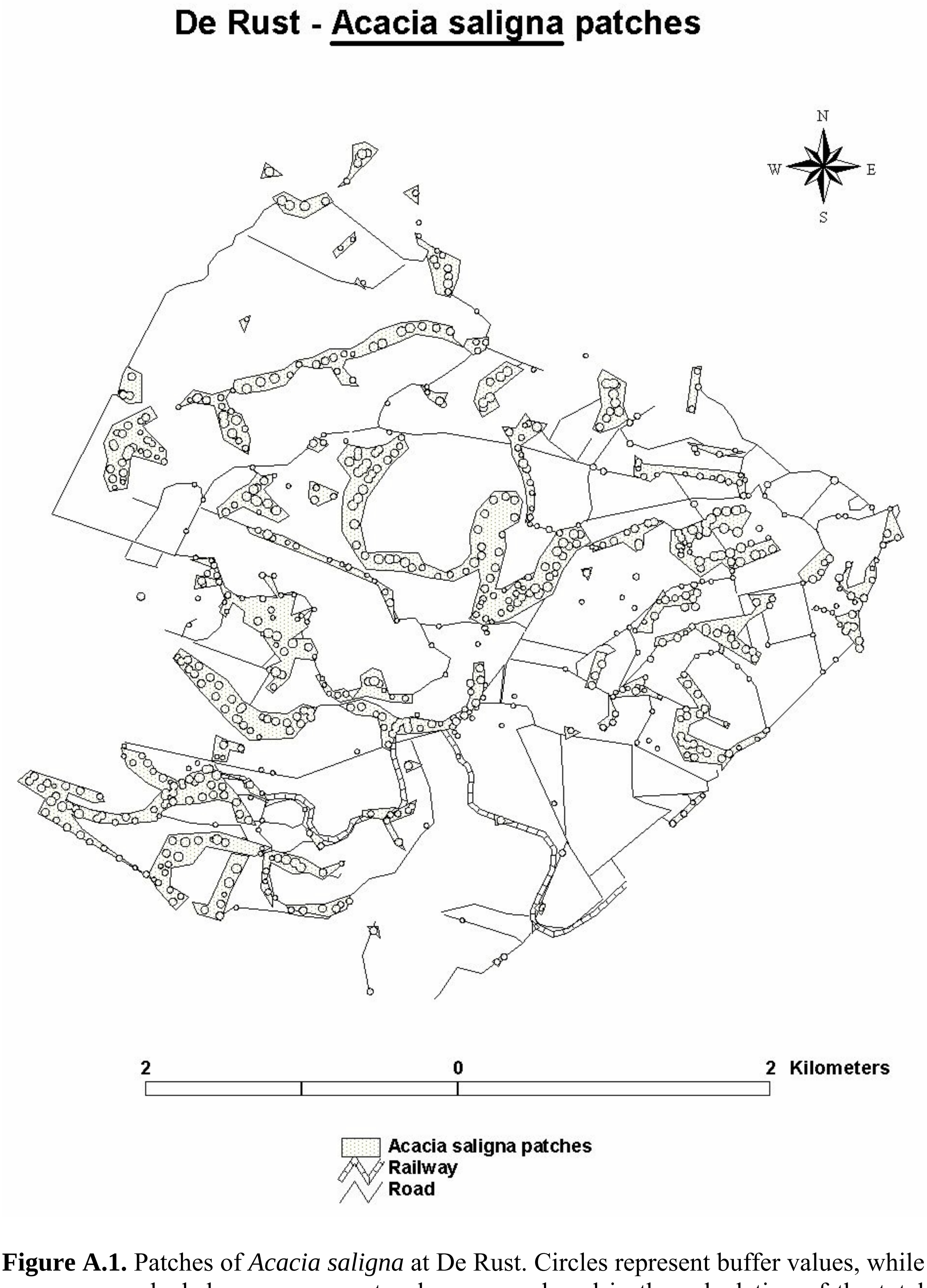

Figure A.1. Patches of *Acacia saligna* at De Rust. Circles represent buffer values, while shaded areas represent polygons employed in the calculation of the total invasion area for the species.

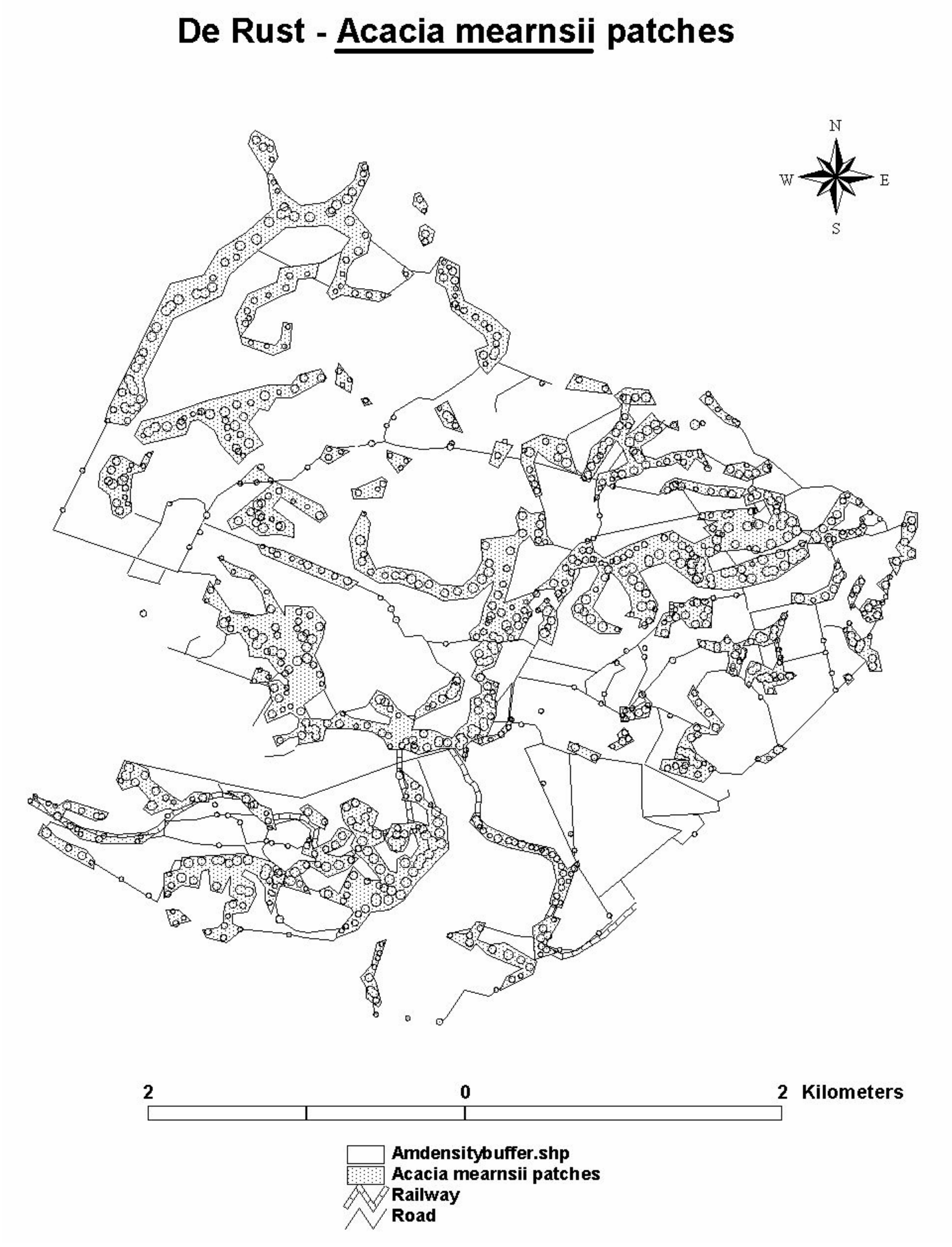

Figure A.2. Patches of *Acacia mearnsii* at De Rust. Circles represent buffer values, while shaded areas represent polygons employed in the calculation of the total invasion area for the species.

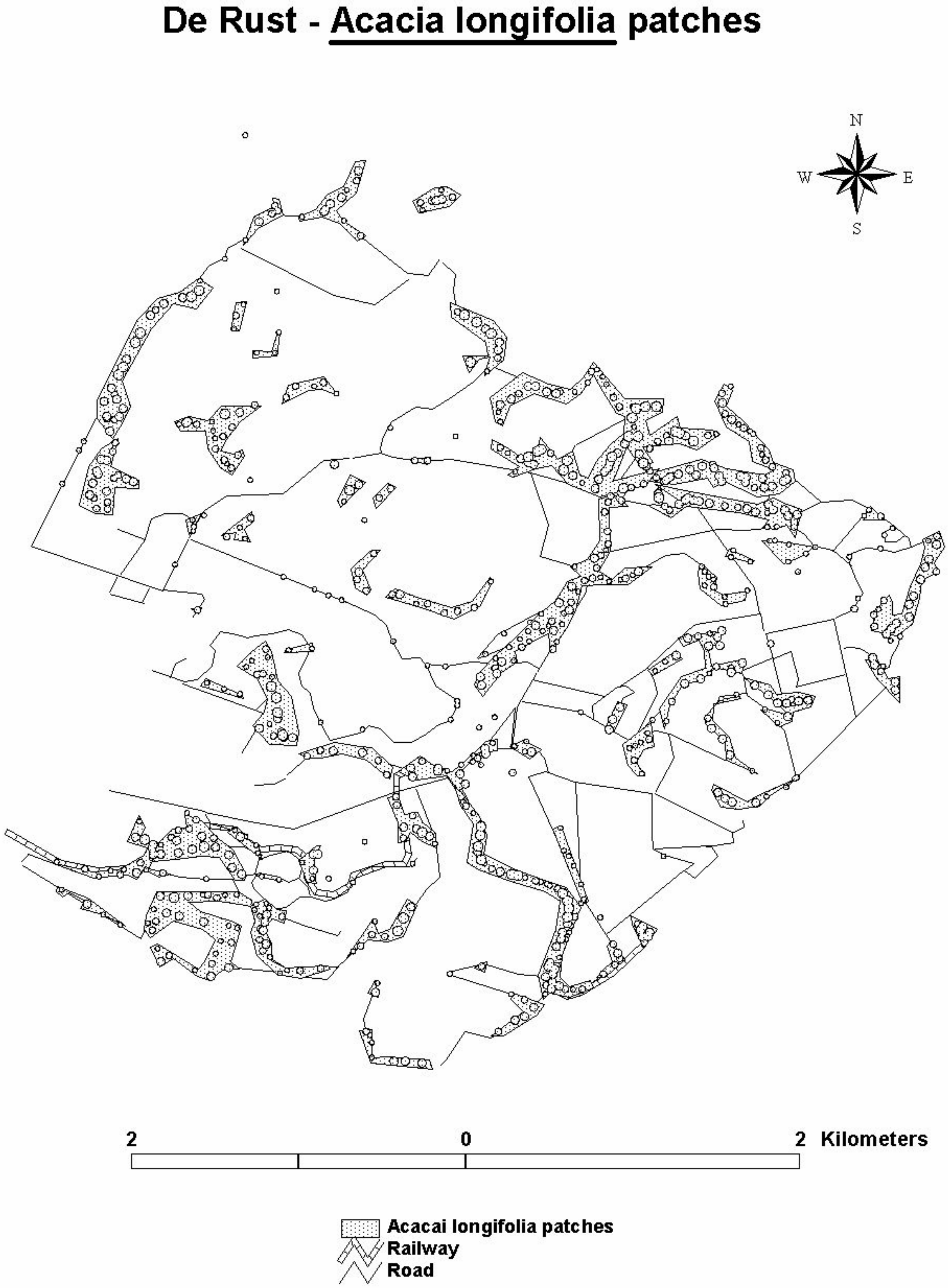

Figure A.3. Patches of *Acacia longifolia* at De Rust. Circles represent buffer values, while shaded areas represent polygons employed in the calculation of the total invasion area for the species.

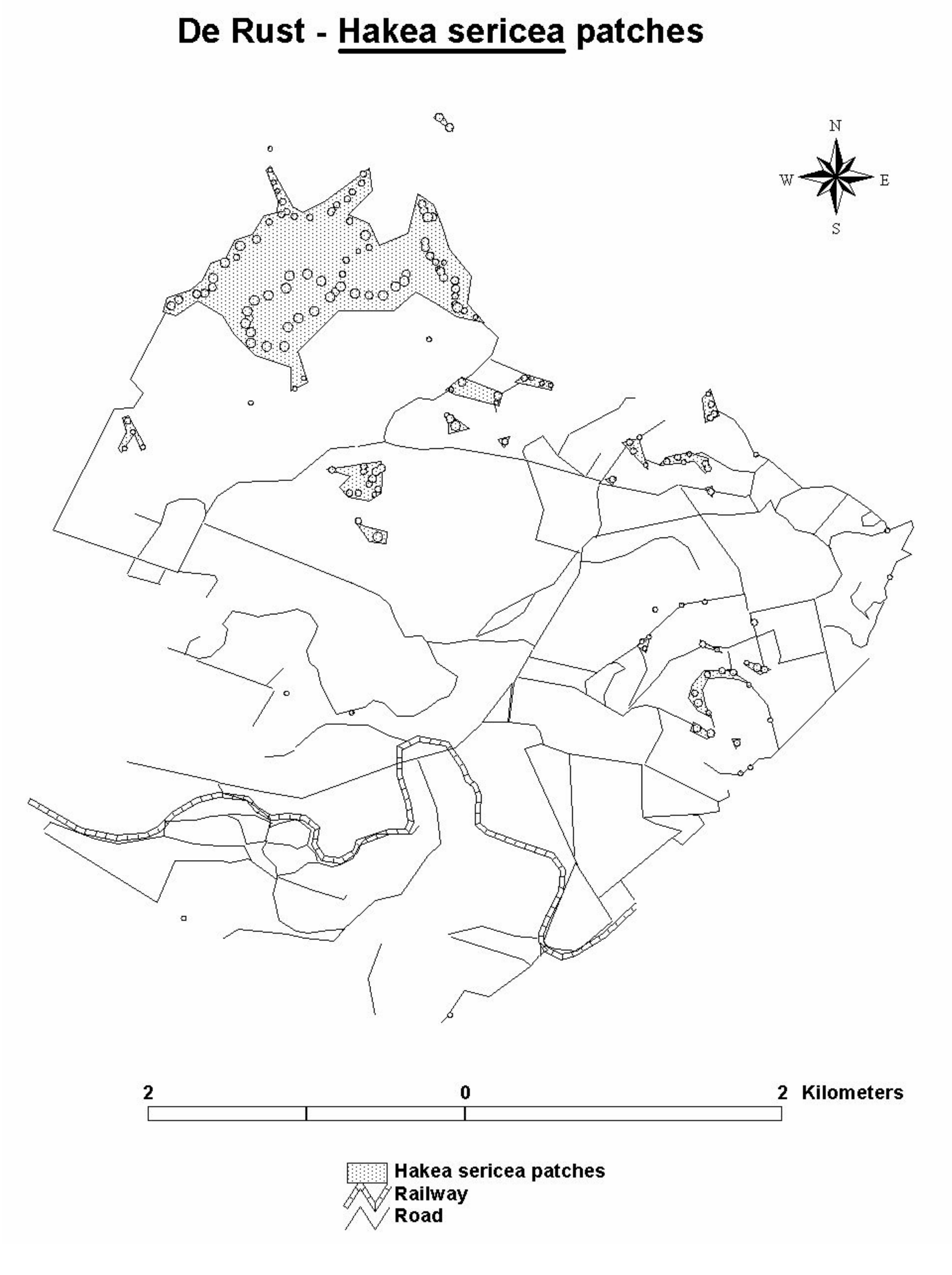

Figure A.4. Patches of *Hakea sericea* at De Rust. Circles represent buffer values, while shaded areas represent polygons employed in the calculation of the total invasion area for the species.

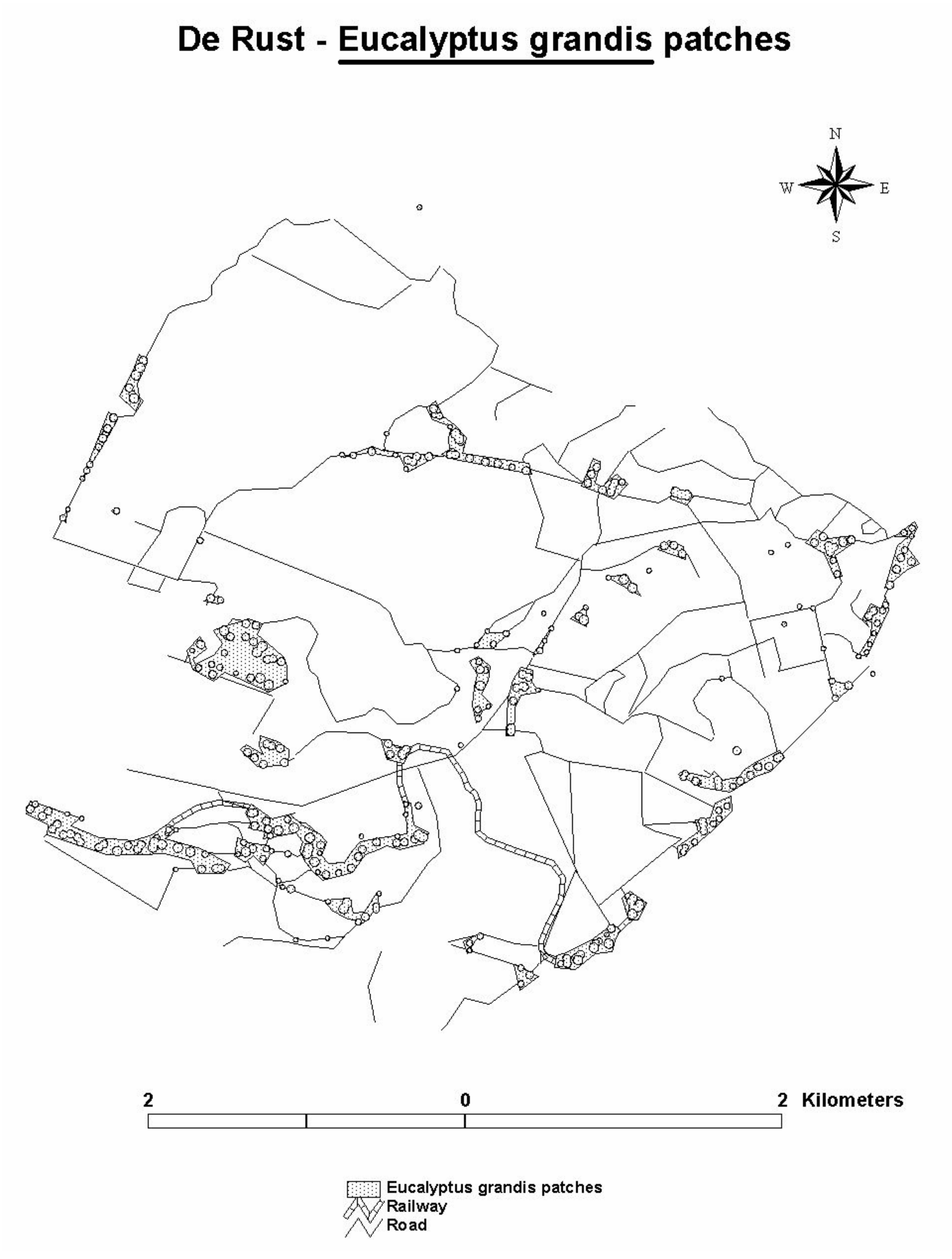

Figure A.5. Patches of *Eucaluptus grandis* at De Rust. Circles represent buffer values, while shaded areas represent polygons employed in the calculation of the total invasion area for the species.

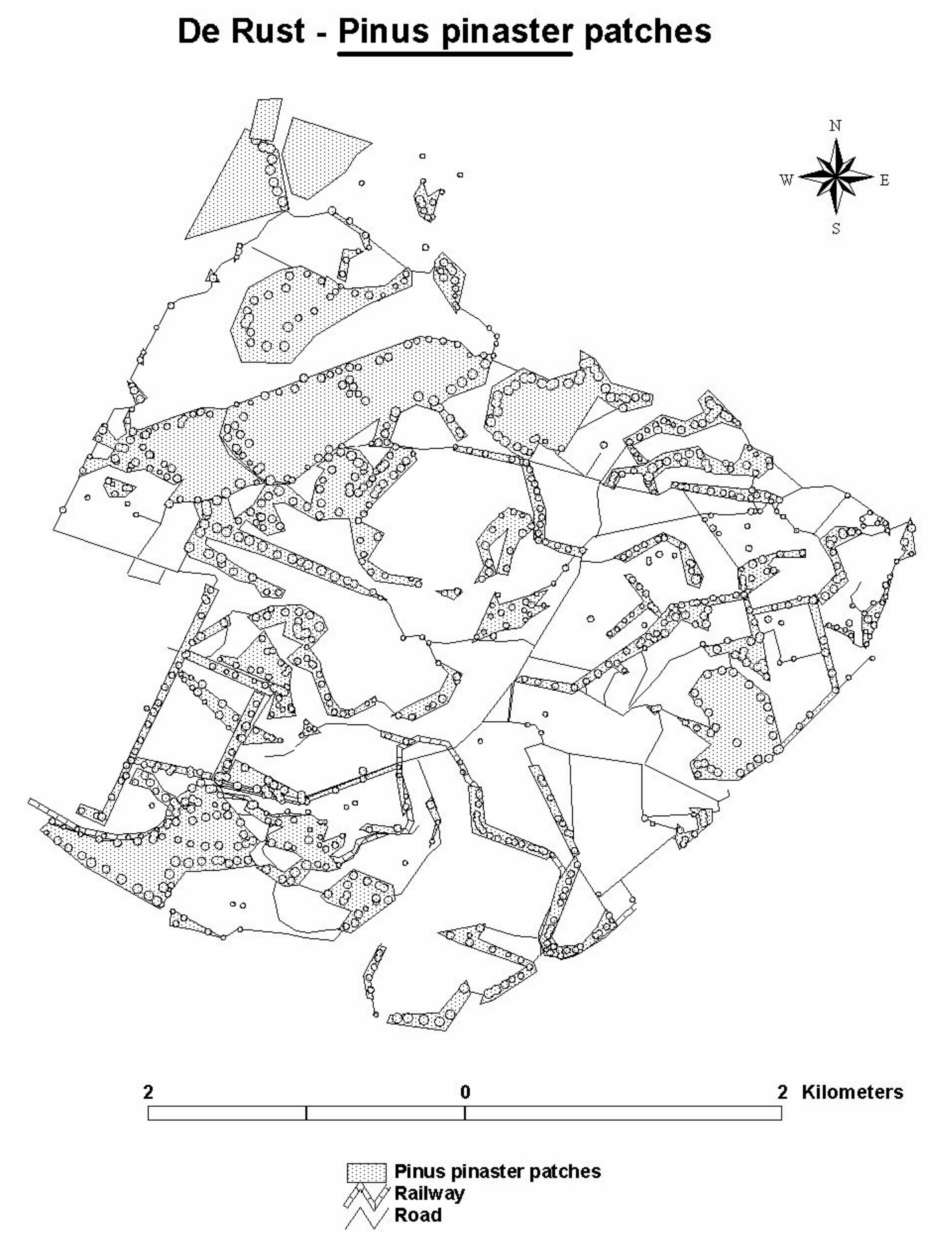

Figure A.6. Patches of *Pinus pinaster* at De Rust. Circles represent buffer values, while shaded areas represent polygons employed in the calculation of the total invasion area for the species.

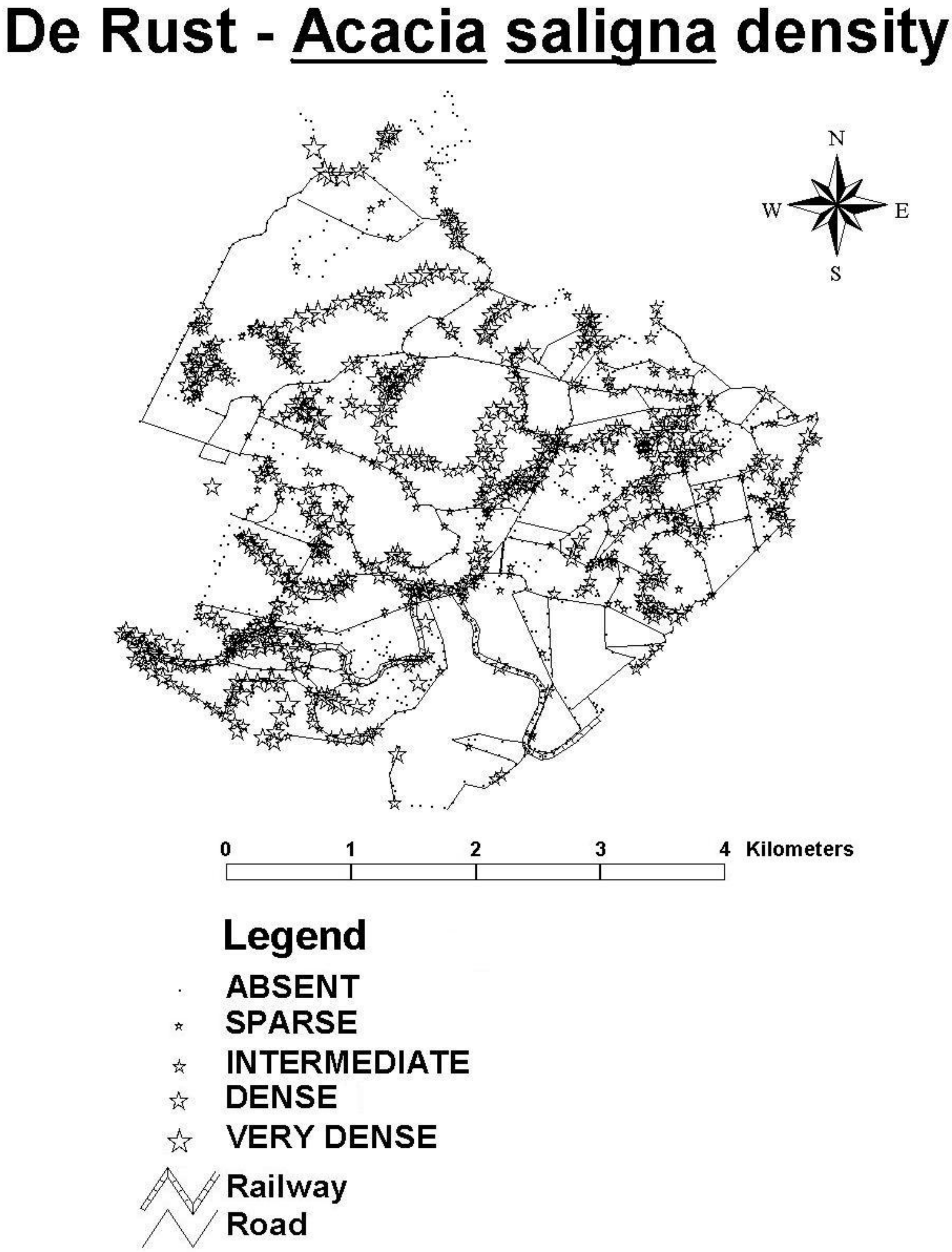

Figure B.1. The distribution of *A. saligna* at De Rust displayed in terms of stand density.

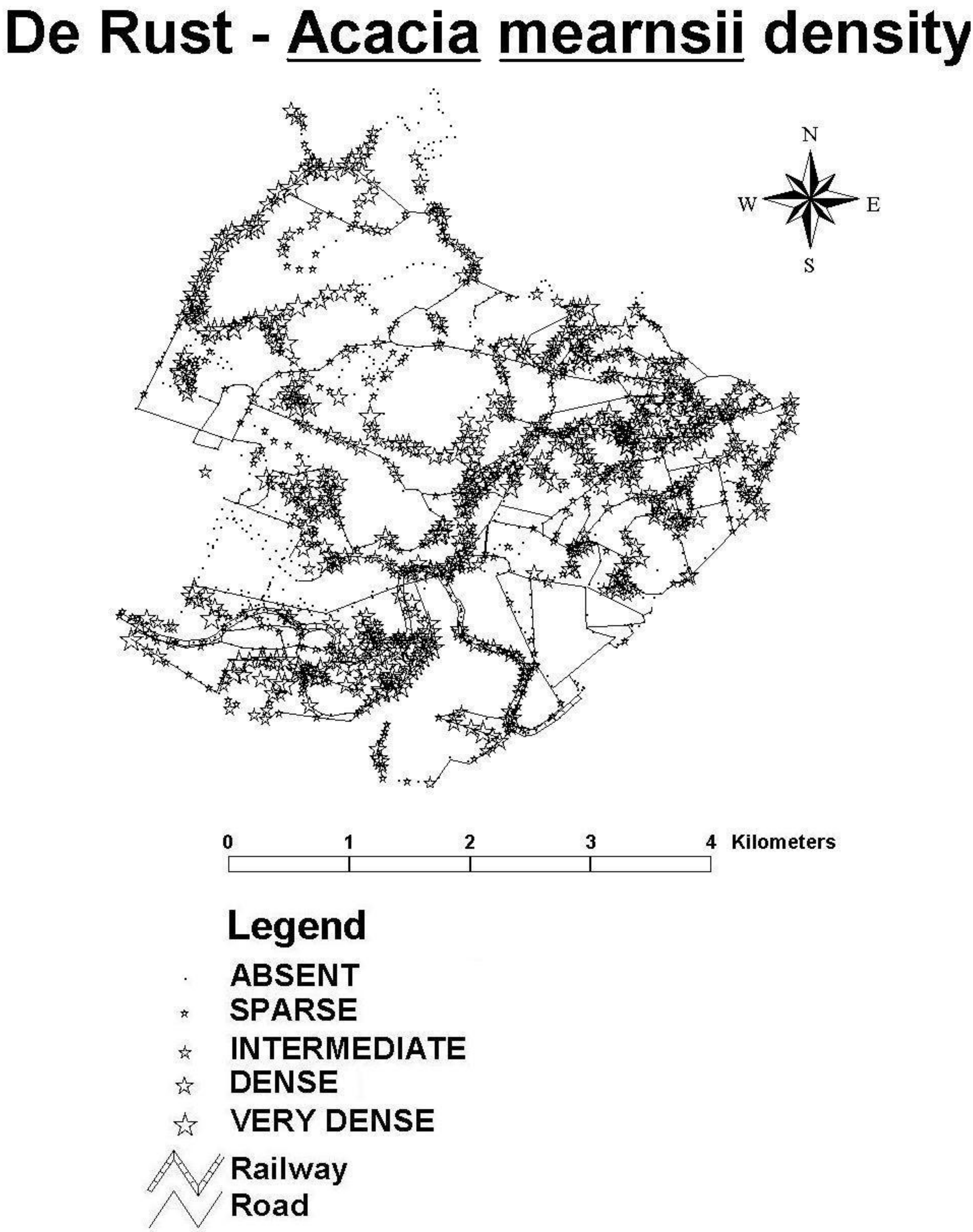

Figure B.2. The distribution of *A. mearnsii* at De Rust displayed in terms of stand density.

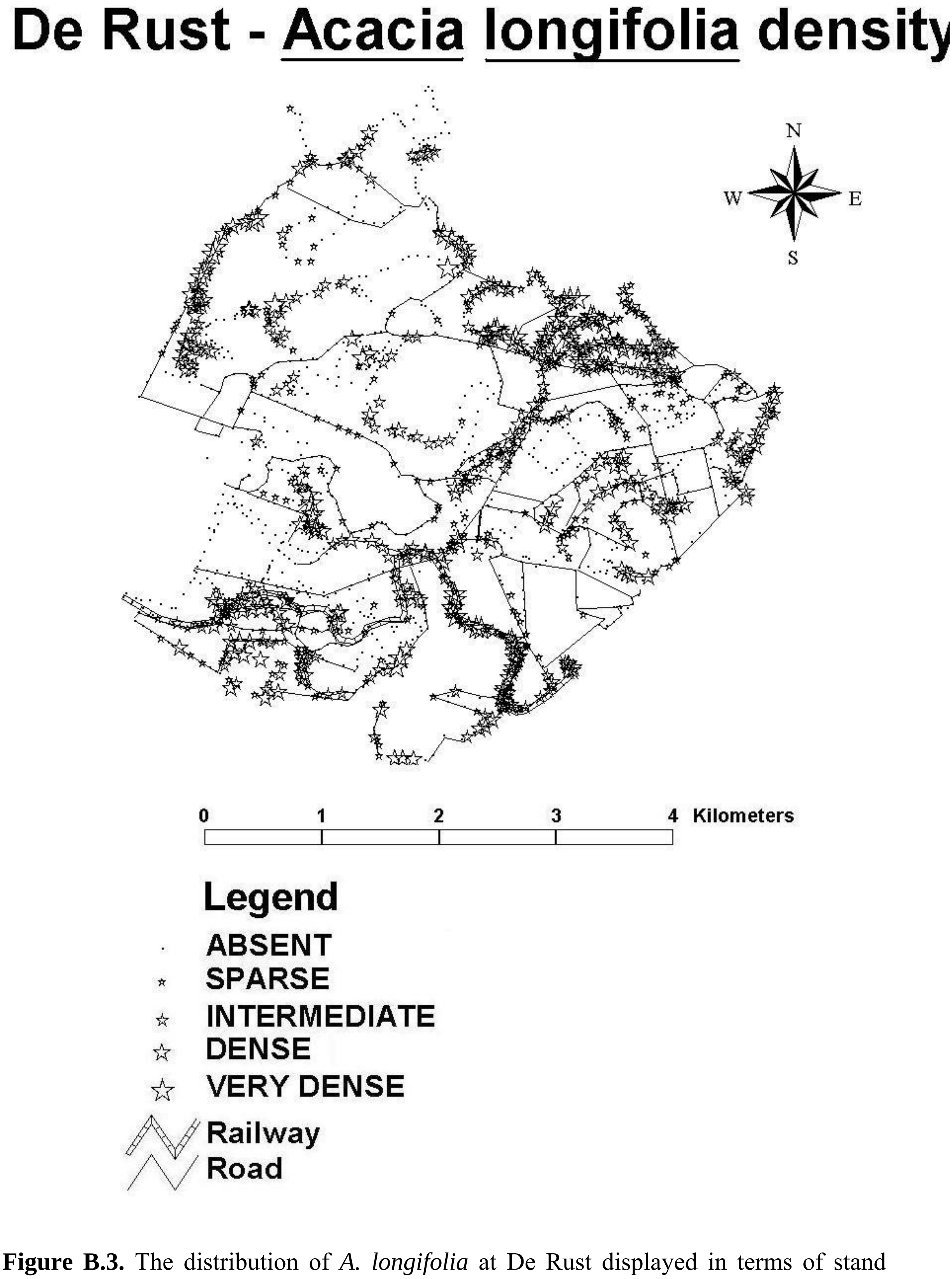

Figure B.3. The distribution of *A. longifolia* at De Rust displayed in terms of stand density.

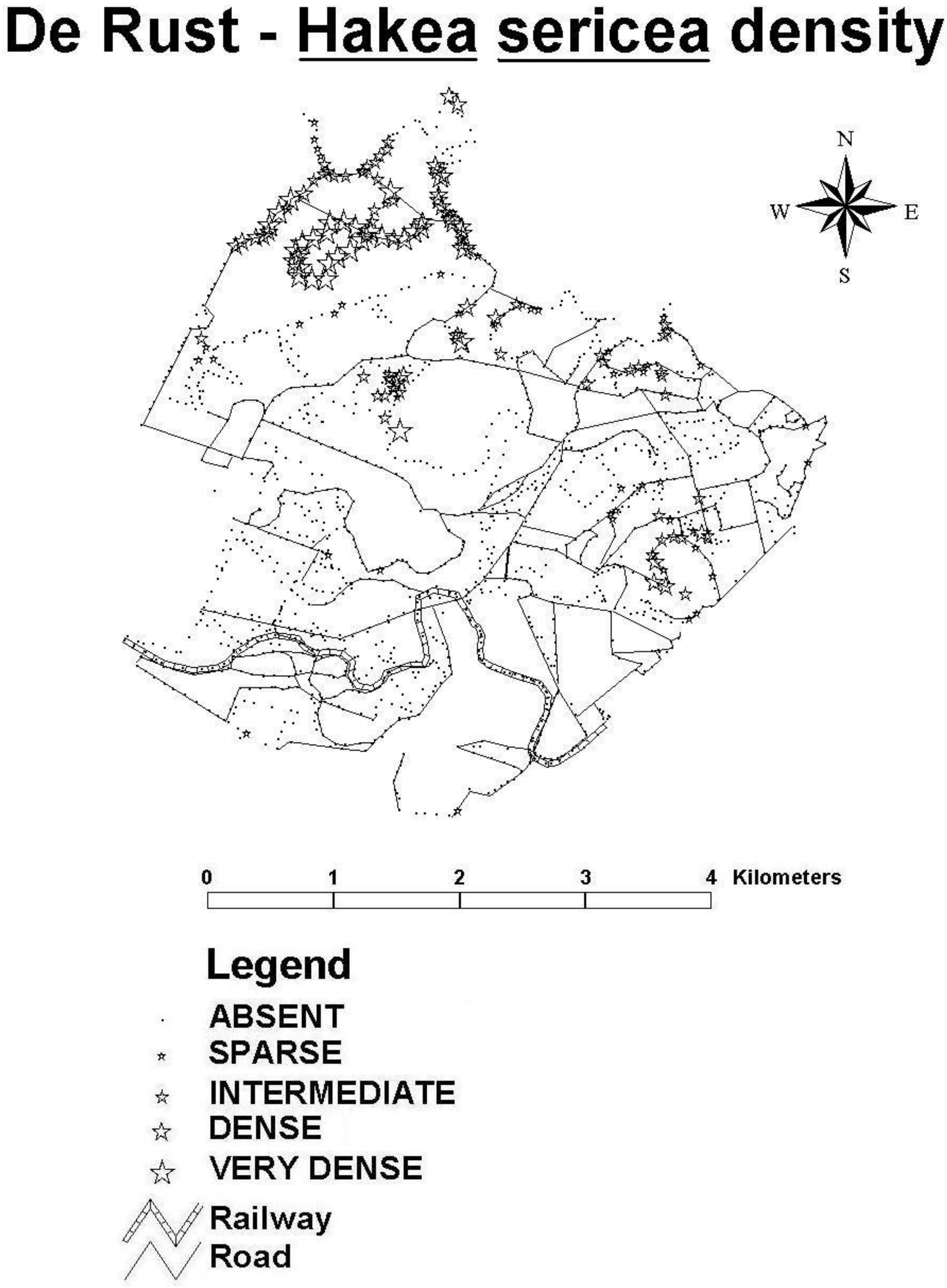

Figure B.4. The distribution of *H. sericea* at De Rust displayed in terms of stand density.

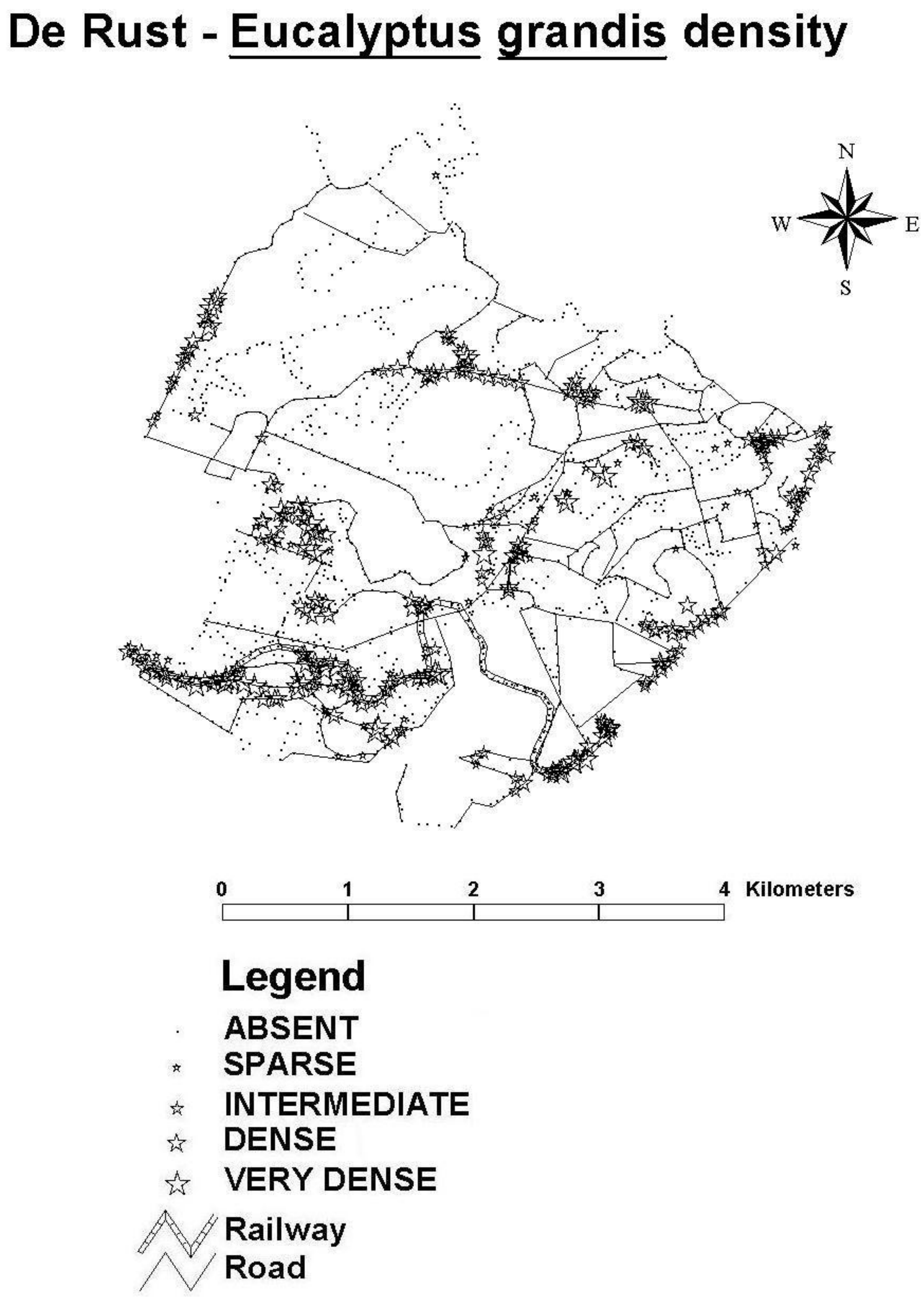

Figure B.5. The distribution of *E. grandis* at De Rust displayed in terms of stand density.

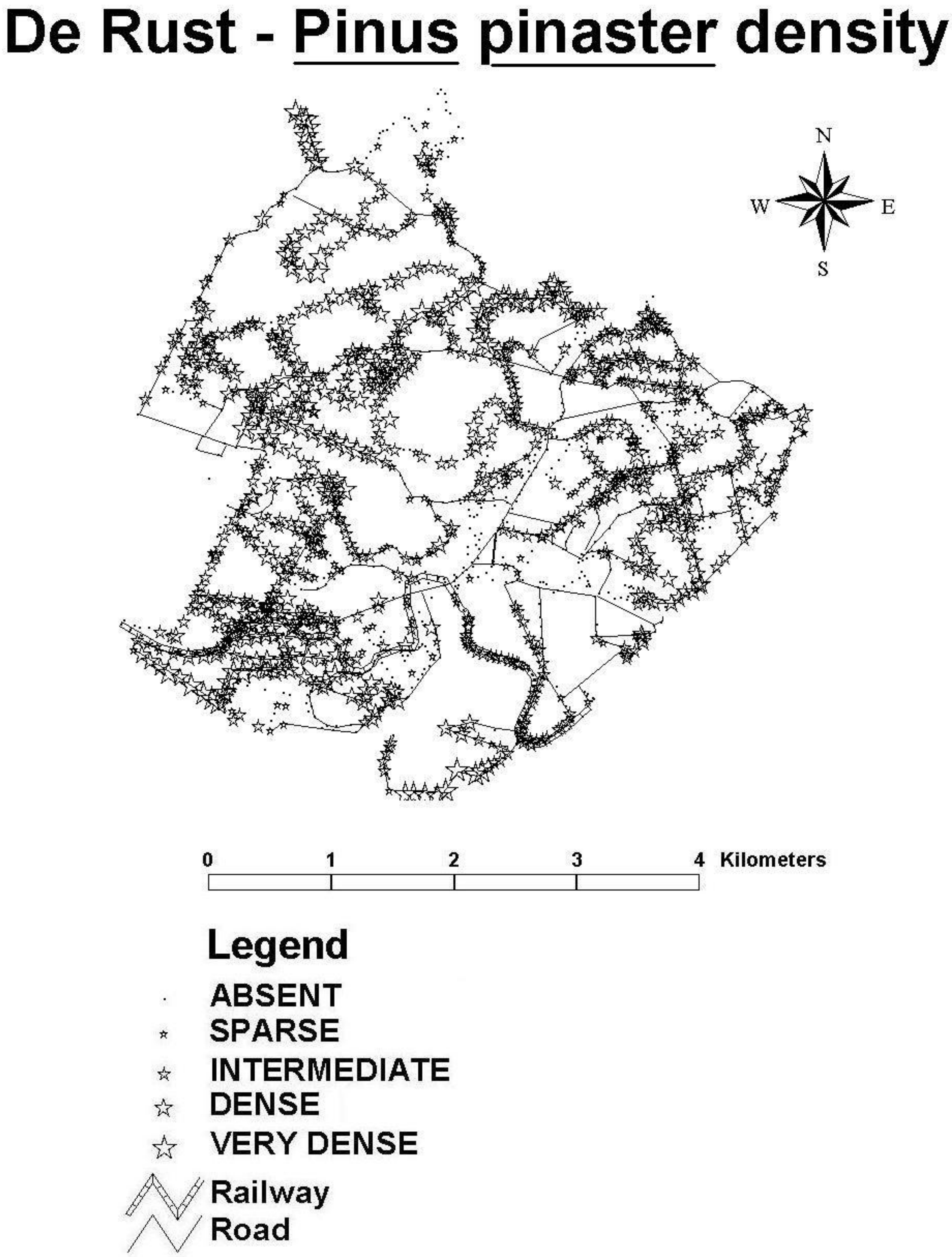

Figure B.6. The distribution of *P. pinaster* at De Rust displayed in terms of stand density.

APPENDIX C: LOG-LIKELIHOOD RATIO ANALYSIS RESULTS

Table C.1. Log-likelihood ratio table of density and land-use for *Acacia saligna*.

Acacia saligna DENSITY				
Land-use category	SPARSE	INTERMEDIATE	DENSE	VERY DENSE
REMNANT PATCH	-21.6	36.4	-19.9	8.8
ROAD	82.4	-5.6	-36.2	-19.6
RIVER	-53.6	-26.3	47.6	67.3
WINDBREAK	12.8	8.5	-12.0	-6.3
VINEYARD+ ORCHARD	10.4	-9.6	1.1	-0.5
RAILWAY+ PROPERTY EDGE	-12.0	13.0	15.0	-5.5
FOREST	5.8	-7.9	18.2	-5.6
DAM	7.3	0.8	0.0	-4.8
			LR statistic	88.6
			P-value	**2.78E-10**

Table C.2. Log-likelihood ratio table of density and land-use for *Acacia mearnsii*.

Acacia mearnsii DENSITY				
Land-use category	SPARSE	INTERMEDIATE	DENSE	VERY DENSE
REMNANT PATCH	-11.2	15.2	-11.1	7.8
ROAD	83.8	7.3	-48.5	-24.7
RIVER	-57.3	-30.2	39.5	81.6
WINDBREAK	35.1	11.8	-14.4	-17.8
VINEYARD+ ORCHARD	-4.8	-2.7	18.4	-8.7
RAILWAY+ PROPERTY EDGE	1.1	23.3	-5.5	-11.2
FOREST	-20.9	-10.9	30.4	20.0
DAM	10.1	-3.3	8.7	-9.2
			LR statistic	101.9
			P-value	**1.31E-12**

Table C.3. Log-likelihood ratio table of density and land-use for *Acacia longifolia*.

Acacia longifolia DENSITY				
Land-use category	SPARSE	INTERMEDIATE	DENSE	VERY DENSE
REMNANT PATCH	-19.2	23.1	-1.4	-1.0
ROAD	32.3	-14.4	-8.0	-6.6
RIVER	-39.3	24.7	26.3	-2.7
WINDBREAK	34.5	0.2	-19.2	1.7
VINEYARD+ ORCHARD	15.5	-6.0	4.5	-5.7
RAILWAY+ PROPERTY EDGE	-7.3	-13.9	8.0	25.6
FOREST	-0.7	-10.7	14.0	5.6
DAM	-1.2	11.1	-7.1	0.4
			LR statistic	63.2
			P-value	**4.10E-06**

Table C.4. Log-likelihood ratio table of density and land-use for *Hakea sericea*.

Hakea sericea DENSITY				
Land-use category	SPARSE	INTERMEDIATE	DENSE	VERY DENSE
REMNANT PATCH	-12.5	2.1	-0.1	13.3
ROAD	1.8	-11.5	-0.6	14.4
RIVER	-7.0	20.2	0.9	-4.8
WINDBREAK	9.8	-3.0	0.9	0.0
VINEYARD+ ORCHARD	1.4	4.2	-1.4	0.0
RAILWAY+ PROPERTY EDGE	5.5	0.0	2.1	0.0
FOREST	4.6	0.2	0.9	0.0
DAM	4.8	-0.5	0.0	0.0
			LR statistic	45.8
			P-value	**1.35E-03**

Table C.5. Log-likelihood ratio table of density and land-use for *Eucalyptus grandis*.

***Eucalyptus grandis* DENSITY**				
Land-use category	SPARSE	INTERMEDIATE	DENSE	VERY DENSE
REMNANT PATCH	5.1	10.3	-23.3	10.9
ROAD	-2.8	8.8	2.9	-7.6
RIVER	2.7	1.4	-5.9	2.3
WINDBREAK	-3.2	15.9	0.2	-3.5
VINEYARD+ ORCHARD	9.5	-2.8	4.0	-3.4
RAILWAY+ PROPERTY EDGE	-9.8	-10.9	9.4	25.9
FOREST	-4.5	-7.0	18.0	0.7
DAM	15.3	-3.6	0.0	0.0
			LR statistic	54.8
			P-value	**7.52E-05**

Table C.6. Log-likelihood ratio table of density and land-use for *Pinus pinaster*.

***Pinus pinaster* DENSITY**				
Land-use category	SPARSE	INTERMEDIATE	DENSE	VERY DENSE
REMNANT PATCH	32.2	1.0	-40.5	11.1
ROAD	8.1	-29.6	-8.6	36.5
RIVER	10.7	-28.7	48.5	-15.3
WINDBREAK	-29.3	151.1	-28.8	7.1
VINEYARD+ ORCHARD	16.2	-7.2	6.7	-6.9
RAILWAY+ PROPERTY EDGE	20.4	-2.9	-18.7	11.7
FOREST	-8.7	-25.9	108.8	0.0
DAM	42.7	-6.7	-11.7	-4.8
			LR statistic	238.2
			P-value	**9.63E-39**

Table C.7. Log-likelihood ratio table of density and land-use fro all species together.

All species DENSITY				
Land-use category	SPARSE	INTERMEDIATE	DENSE	VERY DENSE
REMNANT PATCH	-43.3	112.2	-109.7	49.9
ROAD	188.2	-39.4	-102.9	-25.7
RIVER	-128.0	-84.9	150.7	105.6
WINDBREAK	-49.9	226.9	-83.0	-37.4
VINEYARD+ ORCHARD	64.2	-44.8	34.8	-36.5
RAILWAY+ PROPERTY EDGE	-15.5	-13.4	14.2	17.0
FOREST	-32.6	-73.2	179.1	-6.3
DAM	67.7	-6.6	-15.2	-22.9
			LR statistic	239.4
			P-value	**5.37E-39**

Table C.8. Log-likelyhood ratio table of height and species for roads.

ROAD

Height category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
<1	13.0	-26.9	-2.5	-5.1	-9.9	53.1
<2	-2.3	-49.2	31.9	51.1	-16.6	32.6
<3	-2.1	-33.6	80.4	115.5	-20.4	-37.1
<4	69.5	1.6	55.2	-6.3	-14.8	-39.3
<5	15.2	84.2	28.4	-5.1	-7.5	-53.5
>5	-16.6	-15.4	-23.0	0.0	22.8	104.0
1->5	-43.0	110.0	-62.5	0.0	117.2	33.2
					LR statistic	526.4
					P-value	**4.5E-92**

Table C.9. Log-likelyhood ratio table of height and species for windbreaks.

WINDBREAK

Height category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
<1	1.6	-2.3	-1.1	0.0	15.8	-6.3
<2	15.1	-7.7	12.9	25.7	-3.5	-15.4
<3	6.7	-8.9	43.4	12.2	-3.7	-17.7
<4	11.3	1.6	35.9	0.0	-3.6	-19.2
<5	19.5	52.2	3.2	0.0	-3.7	-26.7
>5	-17.2	-12.8	-8.1	0.0	-6.7	110.2
1->5	-17.9	-1.3	-17.2	0.0	48.3	36.4
					LR statistic	251.1
					P-value	**9.4E-37**

Table C.9. Log-likelyhood ratio table of height and species for dams.

DAM

Height category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
<1	0.4	-6.0	-3.4	5.0	-0.6	13.8
<2	-8.3	-11.0	16.5	-0.3	0.9	14.4
<3	0.2	-4.6	6.9	0.8	-1.2	0.2
<4	19.3	-2.9	5.2	1.3	-1.5	-4.1
<5	6.7	9.4	-0.6	0.0	0.0	-5.2
>5	0.0	-1.2	1.5	0.0	2.7	-1.3
1->5	-7.5	34.6	-4.7	0.0	8.8	-2.1
					LR statistic	82.3
					P-value	**9.3E-07**

Table C.10. Log-likelyhood ratio table of height and species for rivers.

RIVER

Height category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
<1	-2.7	-12.0	0.4	2.2	-2.6	35.0
<2	-8.6	-32.8	17.2	36.4	-7.7	63.6
<3	-14.0	-32.6	40.2	62.8	-8.0	11.1
<4	11.0	-6.3	52.6	-1.6	-6.5	-19.9
<5	31.3	3.2	46.9	0.0	-9.1	-32.2
>5	-6.5	16.0	-19.5	0.0	41.2	8.4
1->5	-4.3	152.7	-59.5	0.0	27.7	-16.5
					LR statistic	357.2
					P-value	**1.2E-57**

Table C.11. Log-likelyhood ratio table of height and species for remnant patches.

REMNANT PATCH

Height category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
<1	1.1	-35.3	-12.3	-6.4	1.1	85.8
<2	-31.0	-81.5	31.0	96.1	-21.1	122.3
<3	-39.9	-68.2	115.0	164.0	-22.5	10.6
<4	90.5	-23.5	117.4	-8.7	-17.4	-60.3
<5	103.7	70.0	55.1	-6.3	-20.7	-96.8
>5	-13.8	6.8	-28.9	0.0	31.5	78.8
1->5	-54.6	287.6	-87.0	0.0	146.7	-27.1
					LR statistic	851.9
					P-value	**8E-160**

Table C.12. Log-likelyhood ratio table of height and species for vineyards and orchards.

VINEYARD + ORCHARD

Height category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
<1	13.7	-13.1	2.0	0.0	-4.1	15.8
<2	10.7	-18.6	36.2	1.4	-4.1	-3.6
<3	14.9	-10.0	20.8	19.7	-3.4	-8.4
<4	-3.6	9.9	17.6	2.7	-3.2	-8.0
<5	-3.6	23.0	2.5	0.0	0.3	-7.7
>5	-11.0	-7.4	-12.0	0.0	14.2	50.7
1->5	-10.3	44.8	-28.5	0.0	23.6	4.6
					LR statistic	168.5
					P-value	**3.2E-21**

Table C.13. Log-likelyhood ratio table of height and species for forests.

FOREST

Height category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
<1	7.1	-1.8	9.2	-0.1	0.0	-3.4
<2	14.7	-6.7	5.7	20.2	0.0	-5.3
<3	-0.3	-4.9	12.7	29.0	0.0	-3.5
<4	9.6	-3.6	8.6	-0.2	-1.9	-3.6
<5	7.5	-5.9	20.5	-1.1	-1.7	-5.6
>5	-5.6	-11.8	-6.8	0.0	8.1	42.8
1->5	-18.1	57.7	-19.3	0.0	20.0	8.3
					LR statistic	170.5
					P-value	**1.4E-21**

Table C.14. Log-likelyhood ratio table of height and species for railway lines and property edges.

RAILWAY LINE + PROPERTY EDGE

Height category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
<1	-3.1	-5.3	-0.2	1.3	4.9	9.2
<2	-4.2	-1.4	7.6	9.3	-5.1	4.8
<3	-3.7	1.3	31.6	0.5	-6.2	-7.2
<4	6.2	-4.5	37.5	0.0	-6.3	-8.7
<5	23.6	6.0	15.7	-0.5	-10.3	-13.2
>5	-2.9	2.1	-9.0	0.4	-6.4	35.1
1->5	-5.1	6.6	-20.6	0.0	76.0	4.9
					LR statistic	160.9
					P-value	**7.7E-20**

Table C.15. Log-likelihood ratio table of age and species for roads.

ROAD Stage category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
SEEDLING	-1.5	-2.1	-3.4	0.0	-1.7	17.7
S	134.4	-26.7	-96.2	-23.0	21.0	116.4
A	-27.5	-35.5	319.7	118.6	-22.6	-5.0
AF	22.4	12.1	81.3	-3.0	0.0	0.0
*S	4.8	-3.6	7.1	0.0	-4.3	5.2
*A	-4.1	0.0	-3.9	-1.5	0.4	65.3
*AF	0.9	6.9	0.0	0.0	0.0	0.0
SA	-8.4	-30.9	1.2	48.0	31.7	-12.9
SAF	-4.4	301.4	-21.0	0.0	0.0	0.0
*SA	-13.4	-22.9	-15.6	-3.6	133.3	45.3
*SAF	-2.8	139.6	-4.9	0.0	0.0	0.0
					LR statistic	1228.3
					P-value	**2.7E-224**

Table C.16. Log-likelihood ratio table of age and species for windbreaks.

WINDBREAK Stage category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
SEEDLING	2.9	4.8	0.0	0.0	1.1	-0.3
S	62.5	10.9	-28.1	-7.1	-15.5	20.2
A	-18.8	-6.9	25.0	4.5	-8.3	165.6
AF	4.6	27.5	-2.7	0.0	0.0	0.0
*S	7.3	-1.2	-1.7	0.0	0.0	3.3
*A	0.0	0.0	0.0	0.0	0.0	82.4
*AF	0.0	3.2	0.0	0.0	0.0	0.0
SA	-0.8	-3.3	2.5	-2.2	2.5	5.2
SAF	-1.8	91.7	-5.3	0.0	0.0	0.0
*SA	-1.5	-12.8	-8.5	0.0	28.5	73.2
*SAF	2.2	55.9	0.0	0.0	0.0	0.0
					LR statistic	560.6
					P-value	**1.8E-87**

Table C.17. Log-likelihood ratio table of age and species for dams.

DAM Stage category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
SEEDLING	0.0	0.0	0.0	0.0	0.0	2.6
S	27.6	-12.6	-16.6	0.0	-6.5	29.1
A	-3.5	0.0	52.5	2.0	-1.3	-5.5
AF	-1.5	0.0	29.3	0.0	0.0	0.0
*S	-1.8	4.5	0.0	0.0	0.0	4.1
*A	0.0	0.0	0.0	0.0	0.0	5.1
*AF	0.0	2.6	0.0	0.0	0.0	0.0
SA	-3.9	1.5	3.4	-0.7	-1.8	-1.1
SAF	2.4	31.6	-3.0	0.0	0.0	0.0
*SA	-3.2	-3.8	-2.5	0.0	12.3	5.1
*SAF	0.6	21.2	0.0	0.0	0.0	0.0
					LR statistic	168.6
					P-value	**9.1E-15**

Table C.18. Log-likelihood ratio table of age and species for forests.

FOREST Stage category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
SEEDLING	0.0	1.5	0.2	0.0	5.5	0.0
S	21.6	-10.7	4.2	-1.9	-3.0	-5.0
A	-7.9	-9.9	-0.1	36.9	-4.0	23.0
AF	10.5	-4.0	40.7	0.0	0.0	0.0
*S	1.2	6.3	0.0	0.0	0.0	0.8
*A	0.0	0.0	0.0	0.0	0.0	21.2
*AF	1.9	1.2	0.0	0.0	0.0	0.0
SA	1.3	-10.6	2.7	3.8	29.4	-8.4
SAF	1.0	32.3	-3.0	0.0	0.0	0.0
*SA	3.3	-11.8	-8.6	-2.2	27.6	5.9
*SAF	-5.9	105.6	-4.2	0.0	0.0	0.0
					LR statistic	288.4
					P-value	**2.9E-35**

Table C.19. Log-likelihood ratio table of age and species for remnant patches.

REMNANT PATCHES Stage category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
SEEDLING	-4.6	-6.0	-6.9	0.0	4.7	28.9
S	271.5	-105.4	-144.8	-31.3	18.6	275.4
A	-49.9	-39.4	699.2	187.8	-25.0	-63.1
AF	4.9	28.1	72.3	-2.9	0.0	0.0
*S	-3.1	7.1	-12.1	0.0	-4.8	33.3
*A	0.0	0.0	-2.9	12.0	2.1	55.3
*AF	0.0	8.5	0.0	0.0	0.0	0.0
SA	-14.9	-40.0	-19.1	56.5	49.5	2.7
SAF	-6.3	483.0	-34.5	0.0	0.0	0.0
*SA	-1.8	-34.6	-24.3	-4.5	137.7	19.0
*SAF	-14.4	249.9	-10.8	0.0	0.0	0.0
					LR statistic	2000.5
					P-value	**0.1E-99**

Table C.20. Log-likelihood ratio table of age and species for rivers.

RIVER Stage category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
SEEDLING	0.8	-2.2	0.3	0.0	0.0	4.9
S	157.3	-73.2	-59.2	-11.6	8.2	25.6
A	-28.1	-31.9	368.3	82.2	-12.8	-44.6
AF	-3.6	6.6	66.6	0.0	0.0	0.0
*S	-3.8	7.4	3.0	0.0	-2.8	-2.4
*A	-1.7	0.0	-1.0	0.0	0.5	12.8
*AF	0.0	2.6	0.0	0.0	0.0	0.0
SA	0.7	-29.3	9.4	2.4	-0.7	-6.5
SAF	-13.5	205.1	-15.9	0.0	0.0	0.0
*SA	9.9	-6.7	-2.6	-3.0	35.6	-20.7
*SAF	-14.3	172.6	-7.9	0.0	0.0	0.0
					LR statistic	782.8
					P-value	**3.0E-132**

Table C.21. Log-likelihood ratio table of age and species for vineyards and orchards.

VINEYARD + ORCHARD Stage category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
SEEDLING	1.5	3.8	-0.9	0.0	0.0	-2.0
S	60.1	-25.7	-11.0	0.0	2.5	-18.4
A	-8.9	-10.0	83.0	9.2	-2.9	9.8
AF	1.5	3.7	33.6	0.0	0.0	0.0
*S	12.0	-1.2	8.6	0.0	-1.1	-4.4
*A	-2.8	0.0	-2.2	0.0	1.3	28.6
*AF	3.0	0.0	0.0	0.0	0.0	0.0
SA	2.1	-12.2	43.0	-2.0	6.9	-14.6
SAF	-4.8	58.8	-2.3	0.0	0.0	0.0
*SA	-4.8	-11.0	-7.5	-2.0	33.3	8.0
*SAF	-9.4	118.0	-4.7	0.0	0.0	0.0
					LR statistic	365.3
					P-value	**1.7E-49**

Table C.22. Log-likelihood ratio table of age and species for railway lines and property edges

RAILWAY + PROPERTY EDGE Stage category	*Acacia saligna*	*Acacia mearnsii*	*Acacia longifolia*	*Hakea sericea*	*Eucalyptus grandis*	*Pinus pinaster*
SEEDLING	0.0	7.3	0.0	0.0	2.3	0.0
S	9.1	-1.3	16.7	0.0	20.1	0.1
A	0.0	-9.8	76.0	5.0	-4.1	12.2
AF	8.4	11.9	6.3	0.0	0.0	0.0
*S	0.0	10.3	0.0	0.0	1.8	0.0
*A	0.0	0.0	0.0	0.0	1.2	13.4
*AF	0.0	0.0	0.0	0.0	0.0	0.0
SA	0.5	-14.6	3.8	-2.7	90.8	-7.6
SAF	9.3	42.4	1.2	0.0	0.0	0.0
*SA	1.6	-5.6	-3.7	0.0	76.6	-4.1
*SAF	0.7	38.2	-2.3	0.0	0.0	0.0
					LR statistic	411.2
					P-value	**3.0E-58**

APPENDIX D: LAND-USE CATEGORY MAPS

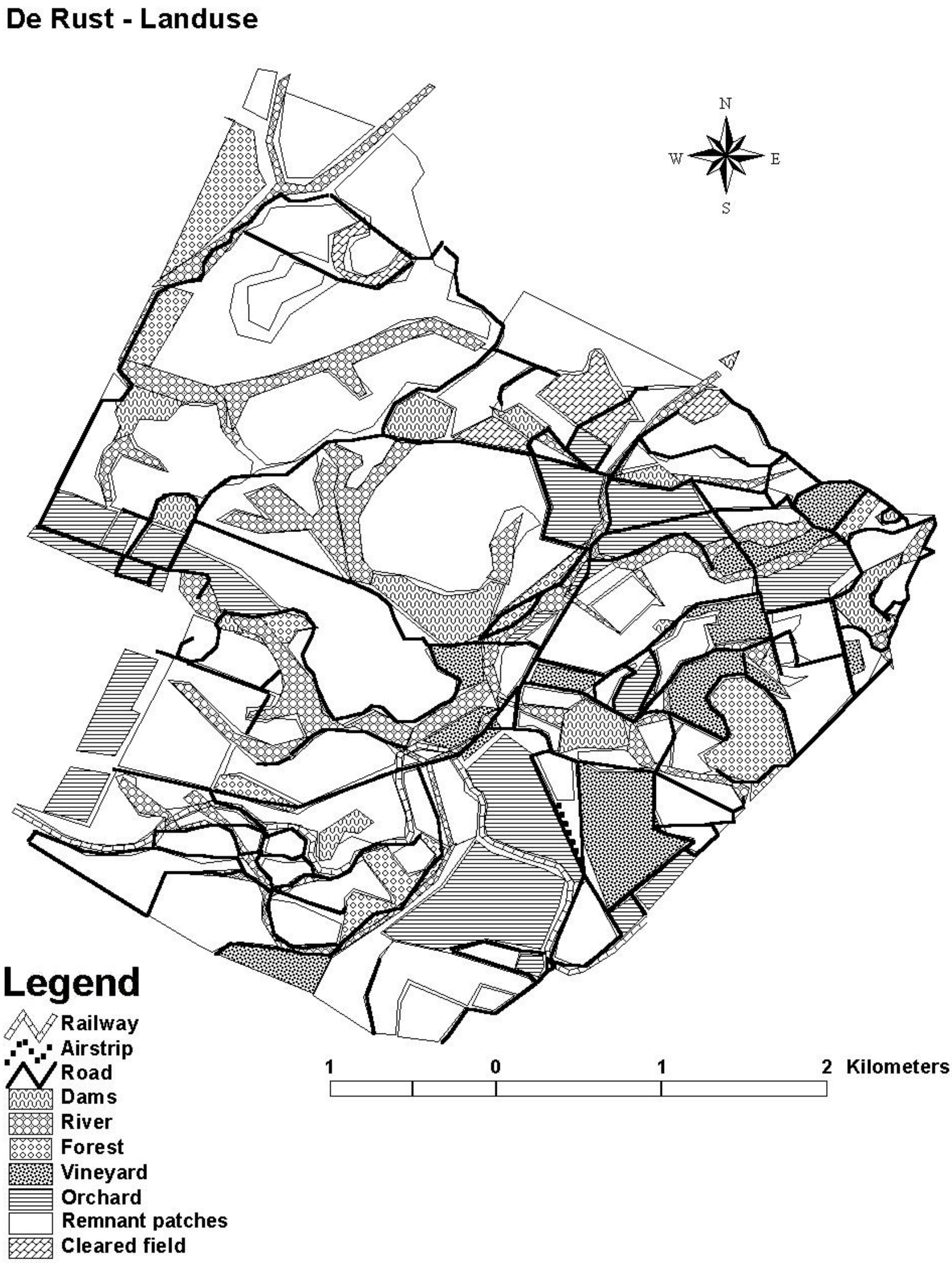

Figure D.1. Fragmentation of all land-use units at De Rust.

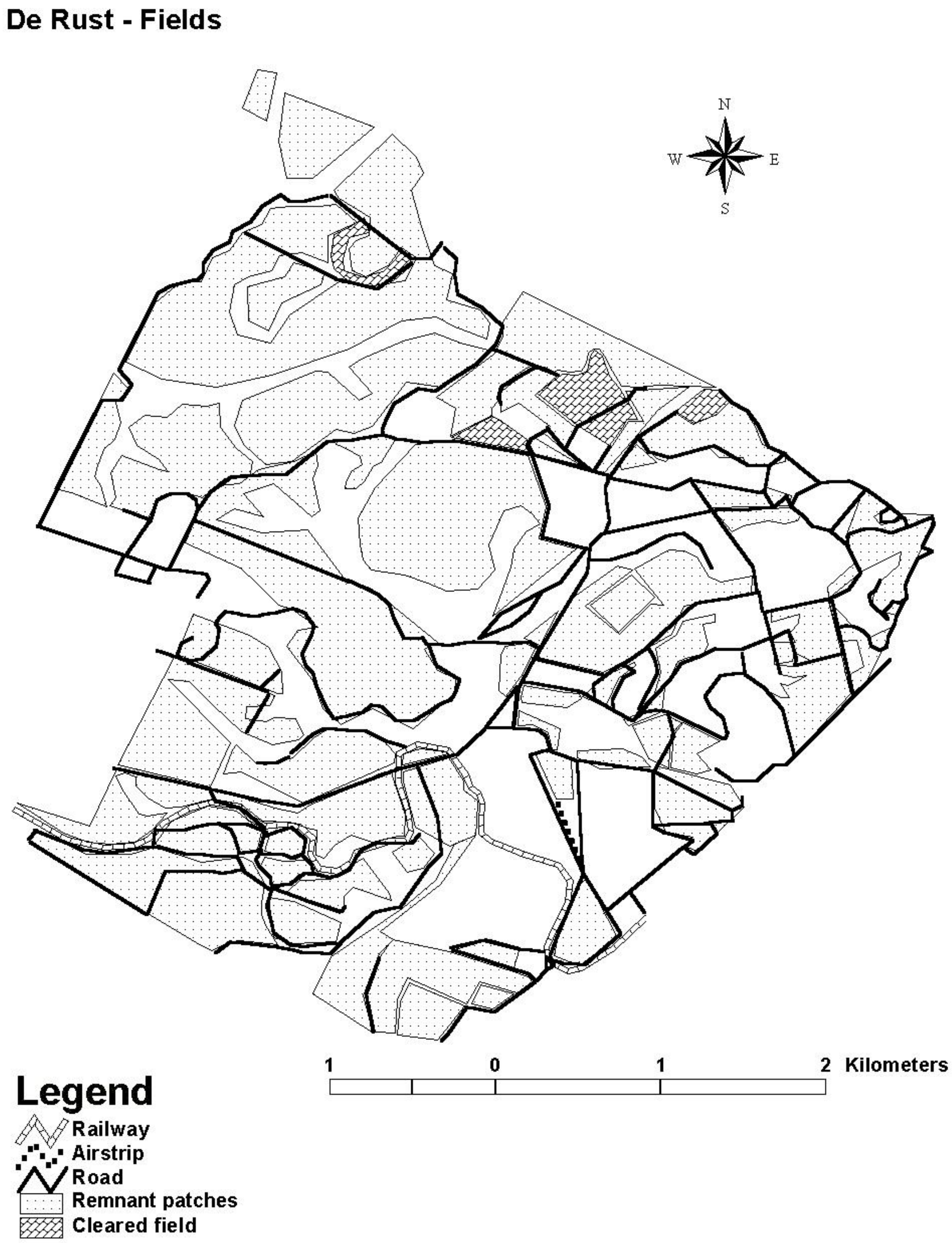

Figure D.2. Fragmentation of remnant patches at De Rust, displaying areas of invasive plant clearing activities.

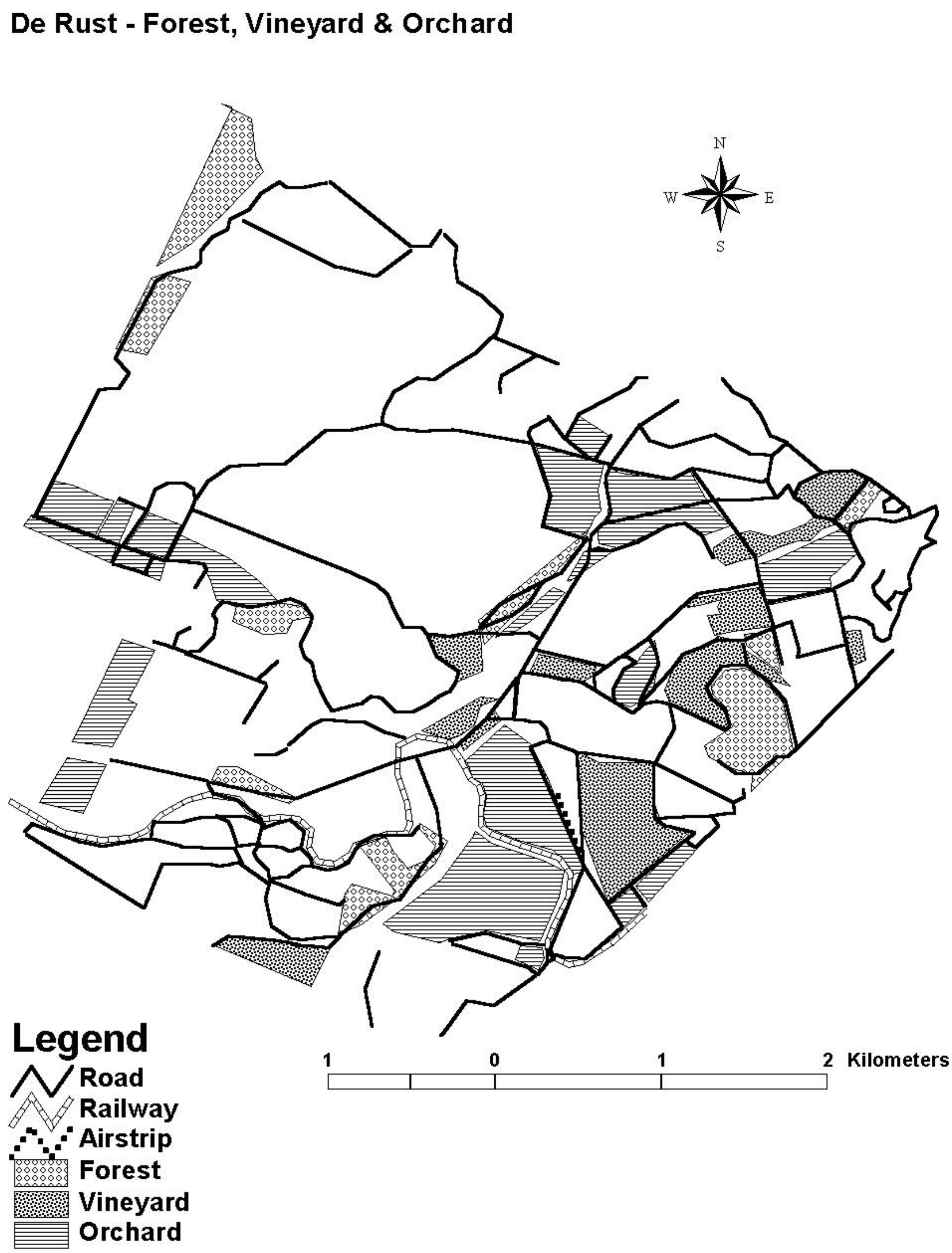

Figure D.3. Areas of economic importance at De Rust.